2009

Scyphozoan jellies as prey for leatherback sea turtles off central California

Tanya R. Graham
San Jose State University

Follow this and additional works at: https://scholarworks.sjsu.edu/etd_theses

SCYPHOZOAN JELLIES AS PREY FOR LEATHERBACK SEA TURTLES OFF

CENTRAL CALIFORNIA

A Thesis

Presented to

The Faculty of Moss Landing Marine Laboratories

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Tanya R. Graham

August 2009

UMI Number: 1478582

UMI®

Dissertation Publishing

ProQuest®

MOSS LANDING MARINE LABORATORIES
SAN JOSÉ STATE UNIVERSITY

The Undersigned Faculty Committee Approves the

Thesis of Tanya R. Graham:

SCYPHOZOAN JELLIES AS PREY FOR LEATHERBACK SEA TURTLES IN
CENTRAL CALIFORNIA
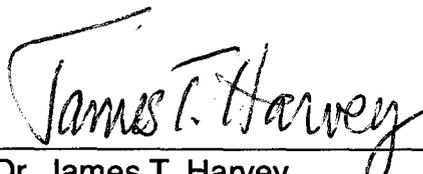
Dr. James T. Harvey,   Moss Landing Marine Laboratories   5/11/09   Date

Dr. Erika McPhee-Shaw,   Moss Landing Marine Laboratories   5-11-09   Date

Dr. David A. Demer   NMFS Southwest Fisheries Science Center   5-11-09   Date

APPROVED FOR THE UNIVERSITY

Associate Dean   Office of Graduate Studies and Research   7/20/09   Date

ABSTRACT

SCYPHOZOAN JELLIES AS PREY FOR LEATHERBACK SEA TURTLES OFF CENTRAL CALIFORNIA

by Tanya R. Graham

Size and nutritional value of four species of scyphozoan jelly (*Aurelia* spp., *Chrysaora colorata*, *Chrysaora fuscescens*, and *Phacellophora camtschatica*) were examined as prey for leatherback turtles (*Dermochelys coriacea*) in a central California foraging area. *Chrysaora fuscescens* and *C. colorata* were larger and more nutritionally beneficial than *Aurelia* spp. and *P. camtschatica*, and jellies contained more carbon and nitrogen during the post-upwelling season when turtles were most abundant. This indicates leatherback turtles maximized foraging success by timing their arrival when prey was larger, more abundant, and more nutritionally beneficial than during other seasons.

Acoustic sampling techniques were developed to characterize the distribution and abundance of scyphozoan jellies in the leatherback turtle foraging area off central California. Acoustic target strength (TS, dB re 1 m^2) values were estimated for scyphozoan jellies using a distorted-wave Born approximation scattering model (mean = -61.9 at 38 kHz and -70.5 at 200 kHz) and *in situ* data (mean = -54.9 at 38 kHz and -63.7 at 200 kHz). Using these data, an algorithm was developed to identify acoustic backscatter from jellies that can be used to characterize the distribution and abundance of scyphozoan prey for leatherback turtles in central California.

ACKNOWLEDGEMENTS

INTRODUCTION

This thesis is divided into two independent chapters which each address different aspects of the role of scyphozoan jellies as prey for endangered leatherback sea turtles (*Dermochelys coriacea*) off central California. The first chapter discusses the nutritional value of scyphozoan jellies, and the second chapter addresses the acoustic characterization of scyphozoan jellies as prey for leatherback sea turtles. Each chapter has an abstract, an introduction, methods, results, discussion, and literature cited section, with figures and tables embedded within the text.

TABLE OF CONTENTS

LIST OF TABLES – CHAPTER 1

LIST OF FIGURES – CHAPTER 2

LIST OF TABLES – CHAPTER 2

CHAPTER 1:

NUTRITIONAL VALUE OF SCYPHOZOAN JELLIES AS PREY FOR LEATHERBACK SEA TURTLES (*DERMOCHEYLS CORIACEA*) OFF CENTRAL CALIFORNIA

Tanya R. Graham[1], James T. Harvey[1], Scott R. Benson[2]

[1]Moss Landing Marine Laboratories

8272 Moss Landing Road, Moss Landing, CA 95039

[2]Protected Resources Division

Southwest Fisheries Science Center

c/o MLML Norte

7544 Sandholdt Road, Moss Landing, CA 95039

ABSTRACT

This study characterized the nutritional value of four species of scyphozoan jellies (*Aurelia* spp., *Chrysaora colorata*, *Chrysaora fuscescens*, and *Phacellophora camtschatica*) as potential prey for critically endangered leatherback turtles (*Dermochelys coriacea*) off central California. Jellies were collected via net tows from March through November, 2003 through 2007 ($n = 418$). Elemental analysis of carbon (C) and nitrogen (N) content (% dry weight) indicated the nutritional value. In 2005 (the only year all species were represented), the largest species, *C. fuscescens* (37.9 ± 0.9 cm standard error), also was more abundant. *Chrysaora fuscescens* and *C. colorata* contained more C and N than *P. camtschatica* ($P < 0.01$) and *Aurelia* spp., the latter of which had significantly less C and N than other species ($P < 0.01$). *Chrysaora colorata* ($n = 8$) had an average 14.1 ± 3.4 % C and 3.9 ± 1.4 % N, whereas *P. camtschatica* ($n = 31$) had 9.4 ± 3.5 % C and 2.2 ± 1.0 % N. The oral arms and gonads of *Aurelia* spp., *C. fuscescens*, and *C. colorata* had more C and N than the bell alone ($P < 0.01$) and were more nutritionally beneficial (i.e., greater C and N values) during the post-upwelling season (May through October), when turtles were present in greatest abundance. These findings indicate leatherback turtles maximize foraging success off central California by migrating to the area during the post-upwelling period, when scyphozoan jellies are larger, more abundant, and more nutritionally beneficial than during the earlier upwelling season.

INTRODUCTION

The leatherback turtle (*Dermochelys coriacea*), the largest marine turtle and the only extant species of the family Dermochelyidae, is listed as an endangered species throughout its range (US Endangered Species Act 35 FR 8495, 2 June 1970) and is on the verge of extirpation in the Pacific (Spotila et al. 2000). Its survival is threatened by anthropogenic influences at every life stage. Dangers on nesting grounds include egg harvesting, hunting, and habitat loss. During the 1960s and 1970s, the Malaysian leatherback population was devastated by the human harvest of virtually every egg from every nest (Limpus 1995). By 1993, the number of nesting individuals had decreased from greater than 2,900 females to fewer than 20. Debris in the ocean (Carr 1987, Eckert & Luginbuhl 1988, Bugoni 2001) and interaction with fisheries (Eckert 1997, NMFS and USFWS 1998, Spotila et al. 2000, Work & Balazs 2002) threaten nesting and migratory animals. Adult and juvenile leatherback sea turtles have been captured in fishing gear worldwide — from gillnets in Greece (Margaritoulis 1986) to swordfish and tuna nets and longlines off Chile (Frazier & Montero 1990) and the Hawaiian islands (Skillman & Balazs 1992, Julian & Beeson 1998). The cumulative impact of this myriad of causes of mortality greatly affects the remaining Pacific population of leatherback turtles (NMFS & USFWS 1998).

Nesting populations of leatherbacks have declined precipitously throughout the Pacific Ocean. Approximately 30,000 females nested annually on

Mexican beaches in 1980 — about 50% of the global nesting population (Pritchard 1982). By 1995 and 1996, there were fewer than 1,000 females (Sarti et al. 1996). Populations in Costa Rica decreased from 1,300 nesting females in 1988 and 1989 to only 117 a decade later (Spotila et al. 2000). An estimated 2,300 females nest in the south Pacific on the Solomon Islands, Wermon, Vanuatu, and Papua New Guinea (S. Benson, unpub. data), and approximately 2,600 females nest at Jamursba Medi, Papua, possibly making it the largest remaining nesting population in the Pacific Ocean (Suwelo et al. 1994).

This highly migratory species, found from 60 °N to 42 °S in the Pacific (Stinson 1984), spends nearly its entire life in pelagic waters, making studies of foraging habits challenging. Most of our knowledge of leatherbacks and sea turtles in general comes from studies of nesting females, because nesting individuals are easier to access than individuals at sea and are somewhat predictable in their occurrence. We have huge gaps in our understanding of the pelagic life stage and minimal knowledge of foraging behaviour of non-breeding females or males at any stage beyond hatchling. Our understanding of foraging habits has been limited to stomach content analyses and opportunistic observations, which indicate that adult leatherbacks feed on scyphozoan jellies, salps, pyrosomas, and other soft-bodied invertebrates (Carr 1967, Eisenberg & Frasier 1983, Holland et al. 1990, Work & Balazs 2002).

Small groups of leatherbacks feed seasonally in coastal waters (Starbird et al. 1993, James & Herman 2001, Benson et al. 2007a, 2007b). Inshore waters off California, between Pt. Arena and Pt. Conception, are visited annually by approximately 150 to 180 leatherback turtles exclusively from western Pacific nesting beaches (Dutton et al. 1999, 2007, Benson et al. 2007a, 2007b). They undergo a 6,000 km trans-Pacific migration arriving after conditions favorable to upwelling result in increased productivity and development of large aggregations of scyphozoan jellies (Graham et al. 1992, Schwing et al. 2002, Benson et al. 2007a). These aggregations of prey are common in retention areas between Pt. Reyes and Monterey Bay, where leatherback turtles are most frequently encountered and observed feeding (Benson et al. 2007a). The predictable seasonal arrival of leatherback turtles to well-studied central California affords a rare opportunity to study the foraging ecology of adults of both sexes. By characterizing the prey resources available in this foraging habitat, resource managers will be better equipped to make critical habitat designations to protect a portion of one of the largest remaining nesting populations of leatherback turtles in the Pacific.

Despite their gelatinous bodies, jellies can contain nearly 80% as much carbon as the densest copepod populations (Shenker 1984), yet, there are few data about the seasonally abundant scyphozoan jellies that occur off central California. Common species include *Aurelia* spp. (moon jelly, AULA), *Chrysaora colorata* (purple stripe jelly, CHCO), *Chrysaora fuscescens* (brown sea nettle

5

CHFU), and *Phacellophora camtschatica* (egg yolk jelly, PHCA). Distribution is poorly understood, and no data are available on the abundance, size distribution, or nutritional value of these species off central California.

Regurgitated stomach contents and observations of actively foraging individuals in the study area indicate CHFU is more frequently consumed by leatherbacks than other scyphozoan species (S. Benson, pers. comm.). This selectivity may indicate that CHFU are more nutrient-rich prey than other available scyphozoan jellies. Off coastal Oregon and British Columbia, CHFU had greater carbon content than *Aurelia aurita* (Shenker 1985, Larson 1986). This supports the idea that although other factors may be influential, it is likely that nutritional composition is a driving force in prey selection. Currently there are no data available on the nutritional content of CHCO, or PHCA from any location, size, or season, and no data are available from central California for any species, including AULA and CHFU, to test this hypothesis.

Size, relative abundance, and nutritional content of jellies, from different locations and times of year, are likely a reflection of environmental conditions in which the jellies were collected (Schneider & Behrends 1994). We examined the nutritional content of whole AULA, CHCO, CHFU, and PHCA from central California waters collected throughout most of the year, using carbon (C) as an indicator of carbohydrate and nitrogen (N) as an indicator of protein content. We expected all species to be largest and most nutritionally beneficial, in the late

summer and early fall, when leatherback turtles were present in the greatest abundance (Starbird et al. 1993, Benson et al. 2007a). We also expected CHFU, more commonly associated with foraging leatherbacks, to be the most abundant, and contain more C and N than AULA, CHCO, and PHCA.

Foraging leatherbacks have been observed selectively consuming only portions of a jelly; specifically, they appear to consume the oral arms and gonads of CHFU, often leaving the bell of the jelly relatively untouched (J. Harvey & S. Benson, unpubl. data). Shenker (1985) found that gonadal tissue of other scyphozoan jellies had greater C content by dry weight than the bell or oral arms and gonads. We expected oral arms and gonads for all species to have greater C and N content than the bell alone.

METHODS

Data for this study were collected in the nearshore waters off central California from Bodega Bay (38.3 °N) in the north, to the southern edge of Monterey Bay (36.5 °N). Except for the submarine canyon, which roughly bisects Monterey Bay, the study area was primarily shallow, with most depths < 200 m, and contained diverse habitats, including kelp forests, rocky intertidal, deep waters, and coastal shelf. The productive temperate environment was influenced by seasonal oscillations between upwelling and pronounced relaxation (Broenkow & Smethie 1978). Upwelling season is characterized by wind-driven upwelling of cooler, nutrient-rich water from depth to the ocean surface, and typically occurs from early spring to late summer. The post-upwelling season follows when upwelling has ceased and surface waters become warmer, and typically occurs from late summer to early fall (Skogsberg & Phelps 1946). These seasons are defined by environmental conditions, rather than calendar dates. However, for the purpose of this study, upwelling season was defined as March through August, and the post-upwelling period as September through November. The months of December through February were not sampled during this study.

Jellies were collected via net tow aboard the R/V John Martin during cruises conducted March through November, 2003 through 2007, by the Center for Integrated Marine Technologies (CIMT) and by Moss Landing Marine

Laboratories (MLML, Fig. 1) on independent cruises. Samples were collected at 23 locations throughout the sampling area, eighteen were inside Monterey Bay (Fig. 2). Tows were conducted using either a modified tucker trawl (3 m x 2 m opening, 333 µm mesh, CIMT and MLML) or a mid-water trawl (6.1 m square opening, 25.4 mm cod end mesh, MLML). Tows were up to 20 minutes in duration but were terminated if the density of jellies was great enough to potentially cause damage to the net. Jellies were identified to species and bell diameters were measured (± 0.5 cm). If jellies were visible at the surface but failed to be collected by net tow, a dip net was used to haphazardly collect animals. During MLML cruises, a representative sample collected during each tow was individually frozen in zip-top baggies for subsequent nutritional analysis. A scalpel was used to separate bells from oral arms and gonads from a subsample of AULA, CHFU, and one CHFO. PHCA were collected whole, as they were frequently damaged from the tow.

	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
2003	●		●	●	●	●	●	●	●
2004	●		●		●	● ■	●	● ■	●
2005	●		●	●	●	● ■	●	● ■■ ●	●
2006			●	●	●	● ■	● ■	●	●
2007	●		●		● ■	● ■	■	■	●
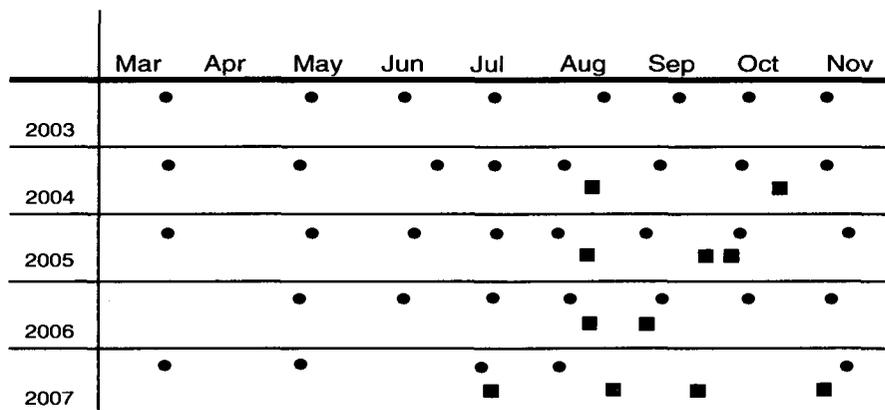
Fig 1. A record of cruise effort aboard the R/V John Martin. Horizontal position of marker indicates approximate date of the cruise within the month noted. (●) Center for Integrated Marine Technologies (CIMT) cruises, (■) Moss Landing Marine Laboratories (MLML) cruises.
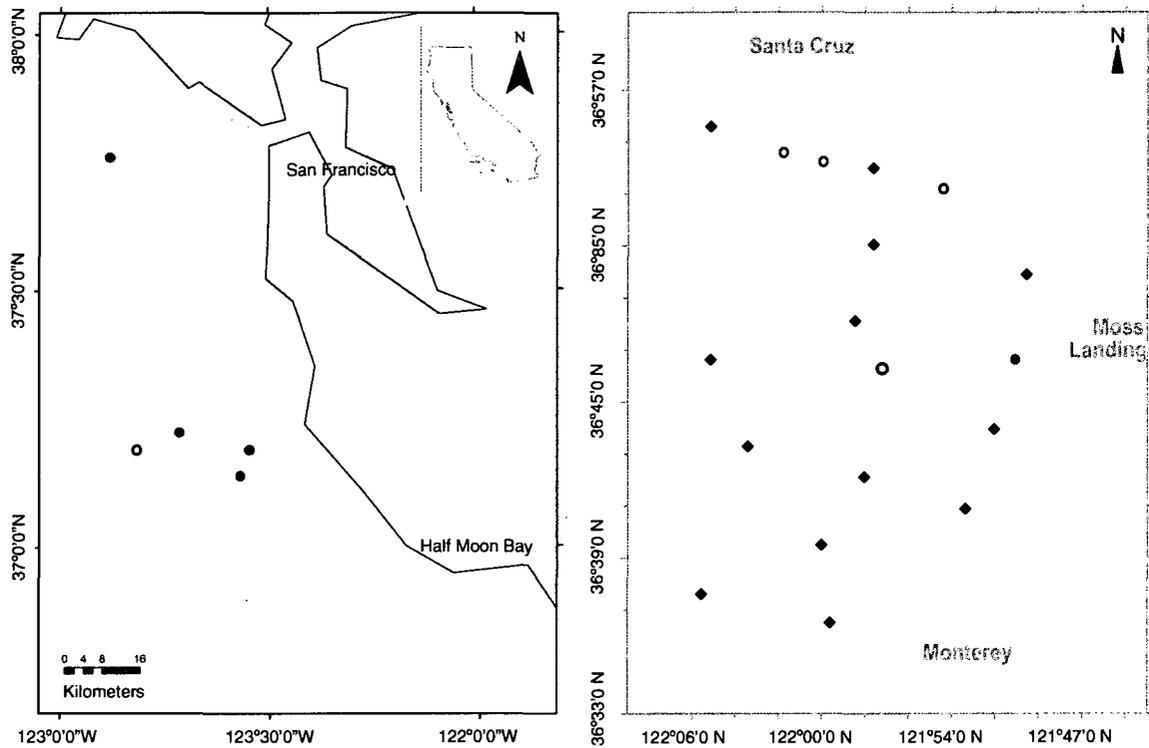
Fig. 2. All net sampling locations off central California. Locations selected for additional analysis of accompanying acoustic data when jellies were present (●) or absent (O), all other tow locations (♦).

Differences in mean bell diameter among species were tested using an analysis of variance (ANOVA). A Tukey, post-hoc, multiple-comparison test was used to determine differences. Species and effort were not equally represented among seasons or years; therefore, comparison of bell diameter between seasons or among years was not possible for all species, and analysis was restricted to 2005 when all species were represented. A nested ANOVA was used to compare mean bell diameter between AULA and CHFU among upwelling and post-upwelling seasons for all years combined. All means are presented ±

one standard deviation (SD), unless otherwise specified. A significance level of α = 0.05 was used for all statistics in this study.

Separated AULA, CHFU, and CHCO, and wholly intact specimens of all four species were randomly selected for elemental analysis of C and N. Jellies were thawed, homogenized, and 7 mL subsamples were poured into clean plastic vials. Vials were frozen at -80 °C and then placed in a lyophilizer for approximately two weeks until the mass stabilized, indicating water loss had ceased. A steel ball mill was then used to homogenize dried samples to a fine powder, and subsamples of approximately 500 µg from each sample vial were measured on a Perkin-Elmer ad-4 Autobalance. Samples were analyzed on a Control Equipment Corporation model 440 elemental analyzer, which uses a thermal conductivity detection method for measuring C and N after combustion and reduction. To ensure dried samples were sufficiently homogenized, a random selection of samples was analyzed in triplicate. Samples were considered well-homogenized if precision of the triplicate samples, estimated by the Coefficient of Variation (CV = standard deviation/mean), was within 10 % of the true mean. A series of blanks and cysteine standards were analyzed before and standards were run again after each 15 to 20 jelly samples were analyzed. Blanks allowed the machine to reach optimum operating conditions and the CV of standards was used to estimate precision of the machine.

Carbon and nitrogen content (expressed as percentage of the dry weight, % DW), and the ratio of C to N (C:N) from whole jellies were compared among species using an Analysis of Covariance (ANCOVA) among all species with bell diameter as a covariate. If the interaction of bell diameter with C, N, or C:N was not significant, the interaction term was removed and the analysis conducted without it. Carbon and nitrogen data were log-transformed to meet assumptions of normality before analyses. If there was a difference among species, a Tukey, post-hoc, multiple-comparison test was used to assess differences. Two-sample t-tests were used to test for differences in mean C %DW, N %DW, and C:N ratio between upwelling and oceanographic seasons for AULA and CHFU.

Differences between mean C and N for body components (bell or oral arms and gonads) of AULA and CHFU were analyzed using parametric and non-parametric statistics. When data were heteroscedastic, randomization tests were used to compare mean C %DW or N %DW within body component between AULA and CHFU (Resampling Stats 6.0). Paired t-tests were used to compare between C %DW and N %DW within each body component of AULA or CHFU. Paired t-tests also were used to compare C %DW or N %DW between body components within species.

RESULTS

Jellies were collected from March 2003 through November 2007 ($n = 418$,

Table 1). All four scyphozoan species common to the central California coast

were present in 2005, and there was a significant difference in bell diameter

among species ($P < 0.01$, F = 31.6, Fig. 3). AULA and PHCA, the smallest

species, were not significantly different from each other, but were significantly

smaller than CHCO and CHFU ($P < 0.05$). CHFU had a significantly greater bell

diameter than CHCO ($P < 0.01$). When bell diameters were compared for all

years of the study, however, CHCO had a significantly greater bell diameter than

all other species ($P < 0.02$) and were the least abundant.

Table 1. Mean, standard deviation, and sample size (n) of bell diameter (cm) of
jellies Aurelia_spp. (AULA), Chrysaora colorata (CHCO), Chrysaora fuscescens
(CHFU), and Phacellophora camtschatica (PHCA) for all cruises off central
California from 2003 through 2007.

Year	AULA Mean	SD	n	CHCO Mean	SD	n	CHFU Mean	SD	n	PHCA Mean	SD	n
2003	15.6	8.1	7	-	-	-	24.2	9.4	18	-	-	-
2004	20.6	9.3	10	-	-	-	23.3	9.5	64	-	-	-
2005	26.7	3.6	11	34.4	7.0	8	37.9	5.2	33	23.0	7.9	31
2006	-	-	-	-	-	-	33.7	5.1	10	-	-	-
2007	29.1	6.6	101	-	-	-	21.3	9.6	125	-	-	-
Grand total	27.7	7.4	129	34.4	7.0	8	24.7	10.6	250	23.0	7.9	31
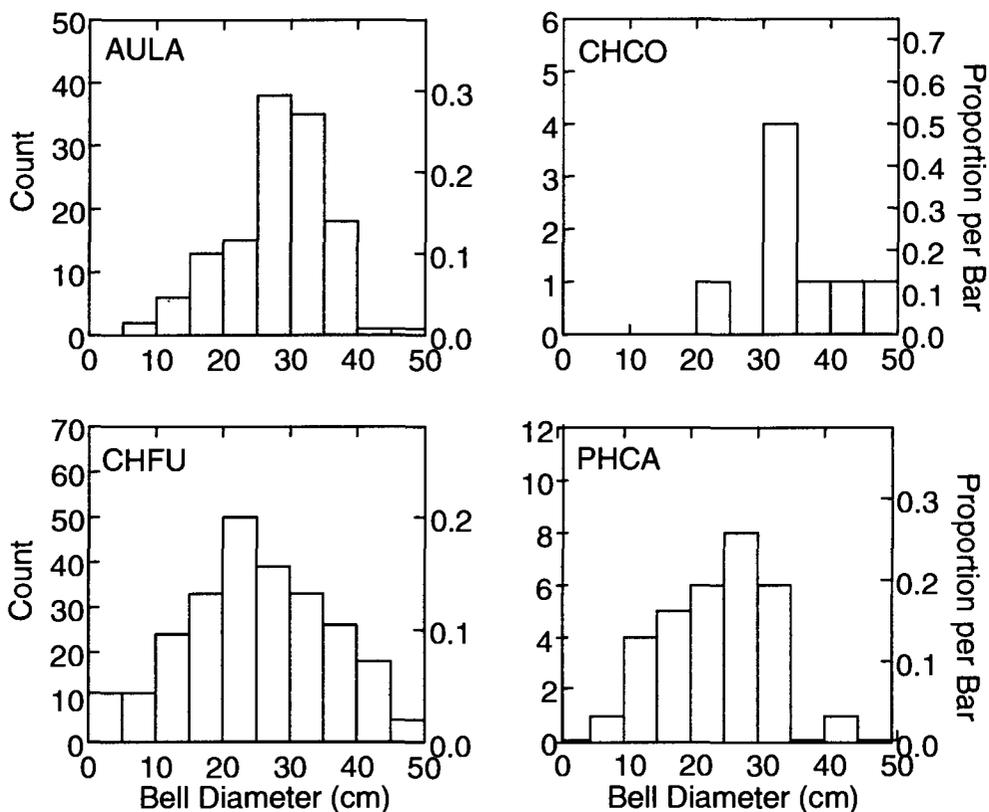
Fig. 3. Distribution of bell diameter (cm) of jellies *Aurelia* spp. (AULA), *Chrysaora colorata* (CHCO), *Chrysaora fuscescens* (CHFU), and *Phacellophora camtschatica* (PHCA) for all cruises off central California from 2003 through 2007.

Comparison of bell diameter between upwelling and post-upwelling seasons was possible for AULA and CHFU, because CHCO and PHCA were collected only during the post-upwelling period. Mean bell diameter of AULA and CHFU was significantly greater during the post-upwelling season (AULA = 30.6 ± 5.7 cm, CHFU = 28.6 ± 8.3 cm) than during upwelling season (AULA = 24.0 ± 7.6 cm, CHFU 18.1 ± 10.8 cm, $P < 0.01$, Fig. 4). Nutritional value (%C and %N) of CHFU was greater in post-upwelling season than upwelling season ($P < 0.01$,

Fig. 5), but the difference was marginal in AULA ($P = 0.10$, Fig. 5). No difference

in C:N was detected for either species between oceanographic seasons.
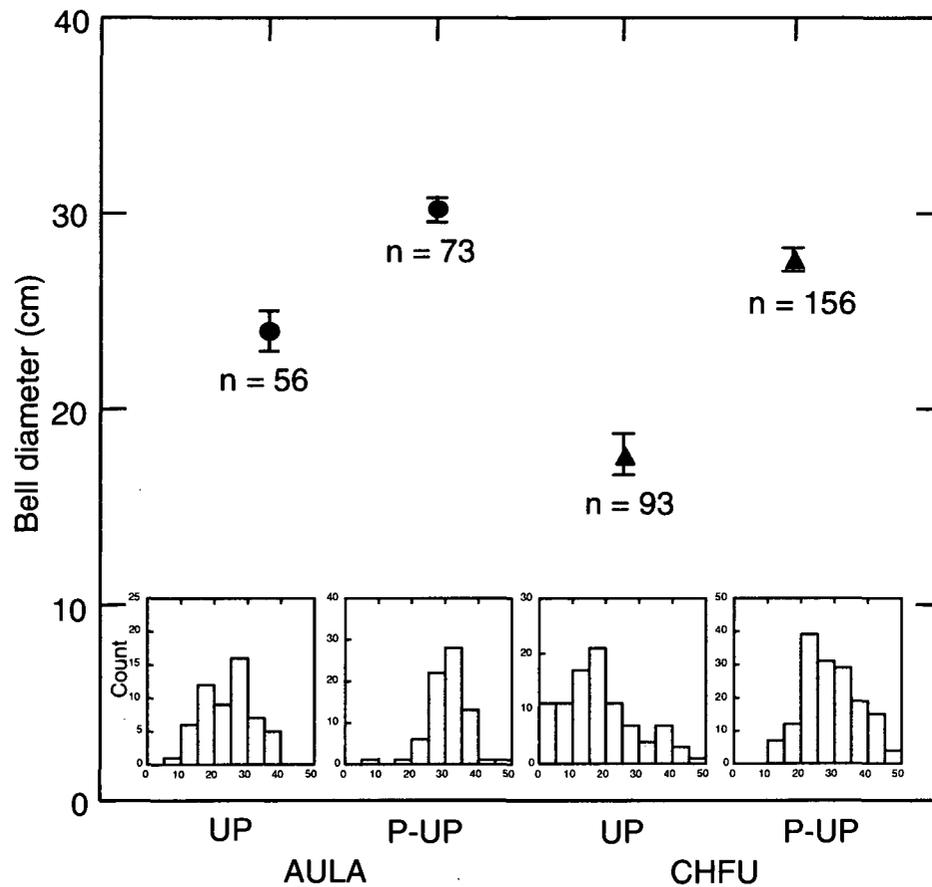
Fig. 4. Mean (± standard error) and distribution of bell diameters and of *Aurelia* spp. (AULA; ●) and *Chrysaora fuscescens* (CHFU; ▲) by oceanographic season (Upwelling = Mar through Aug; Post-upwelling = Sep through Nov) off central California from 2003 through 2007.
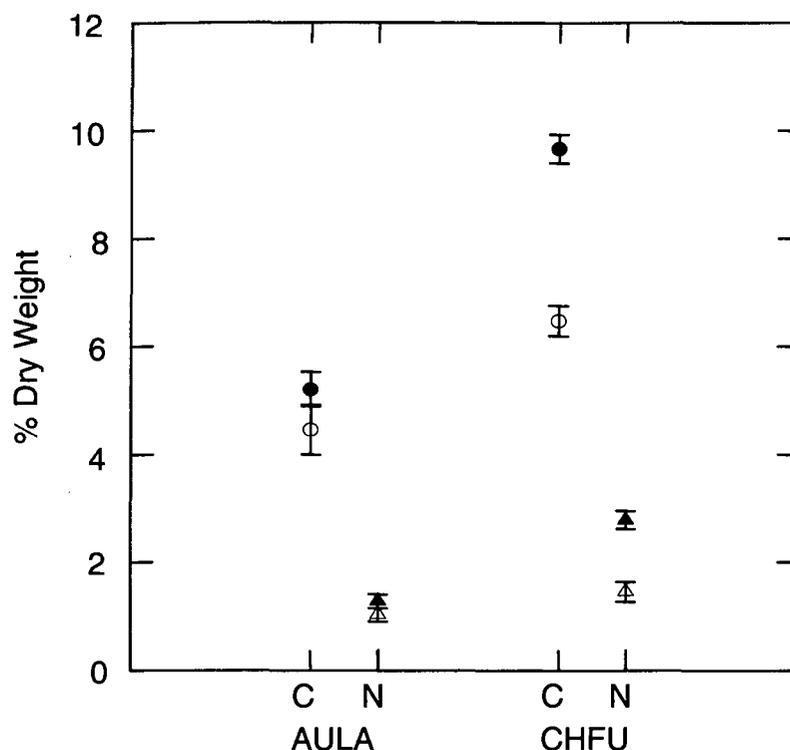
Fig. 5. Mean percentage of dry weight (± standard error) carbon (C; ○) and nitrogen (N; Δ) in AULA and CHFU between upwelling (open symbol) and post-upwelling (closed symbol) seasons. For AULA during post-upwelling season, n = 16, AULA upwelling season, n = 9, CHFU post-upwelling season, n = 9, CHFU upwelling season, n = 19.

Carbon and nitrogen content were significantly different among species ($P < 0.01$). The interaction between bell diameter and C was only marginally significant ($P = 0.05$), and there was no interaction with N so the interaction terms were dropped. AULA contained significantly less C and N than all other species ($P < 0.01$), and there was no difference among CHCO, CHFU, and PHCA (Table 2). The interaction of bell diameter with C:N was not significant, and there was no significant difference in C:N ratio among species.

16

Carbon, nitrogen and C:N ratio were significantly different between bell

and oral arms and gonads for all species ($P < 0.01$, Table 2). Body components

of CHFU had significantly greater C and N than AULA ($P < 0.01$, F = 21.06), but

C:N was greater in AULA. AULA and CHFU had significantly greater C and N in

oral arms than in bells, and C was greater than N in each body component of

both species. The greatest percentage of C and N was in the body components

of CHCO, although only one jelly was sampled so statistical analysis was not

possible.

Table 2. Mean, standard deviation (SD) and sample size (n) of bell diameter (cm), carbon (C) and nitrogen (N; %DW), and ratio of C to N (C:N) of whole jellies (W), oral arms and gonads (OAG), and bell (B) of Aurelia spp. (AULA), Chrysaora colorata (CHCO), Chrysaora fuscescens (CHFU), and Phacellophora camtschatica (PHCA).

Species	Portion	Bell		%C		%N		C:N		
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	n
AULA	W	27.9	5.6	5.5	2.4	1.2	0.5	4.8	1.2	25
	OAG	29.3	6.0	5.5	1.2	1.2	0.3	4.7	0.9	32
	B	29.3	6.0	3.5	1.0	0.7	0.3	4.8	1.0	31
CHCO	W	34.7	5.5	14.1	3.4	3.9	1.4	3.7	0.4	3
	OAG	38.0	-	15.3	0.7	3.7	0.1	4.2	-	1
	B	38.0	-	6.4	<0.1	6.4	<0.1	3.9	-	1
CHFU	W	20.5	7.8	8.2	3.0	1.9	0.9	4.7	0.9	28
	OAG	29.7	8.2	13.8	3.2	3.4	1.0	4.1	0.4	25
	B	29.7	8.2	8.2	4.2	2.1	1.4	4.1	0.6	25
PHCA	W	24.3	7.1	9.4	3.5	2.2	1.0	4.6	0.9	9

Precision (CV), was assessed for the equipment, homogenization, and sample size. Precision of the elemental analyzer was within 3.0 % of the true mean for C values, and within 4.3 % for N values. Adequate precision was obtained for triplicate runs of jelly samples (CV < 10 %), which indicated homogenization of samples was thorough. Variability of C and N content was greater than 10 % in all samples analyzed (Fig. 6). CV stabilized with increased sample size for most AULA and CHFU analyses, which indicated sample size was sufficient and variability was inherent to the population. Precision of C in whole CHCO was 24 % and N was 35 %. Carbon and nitrogen were highly variable and imprecise for PHCA (Fig. 7). Too few PHCA and CHCO were processed to understand if samples were accurate and precise representations of the population variability.
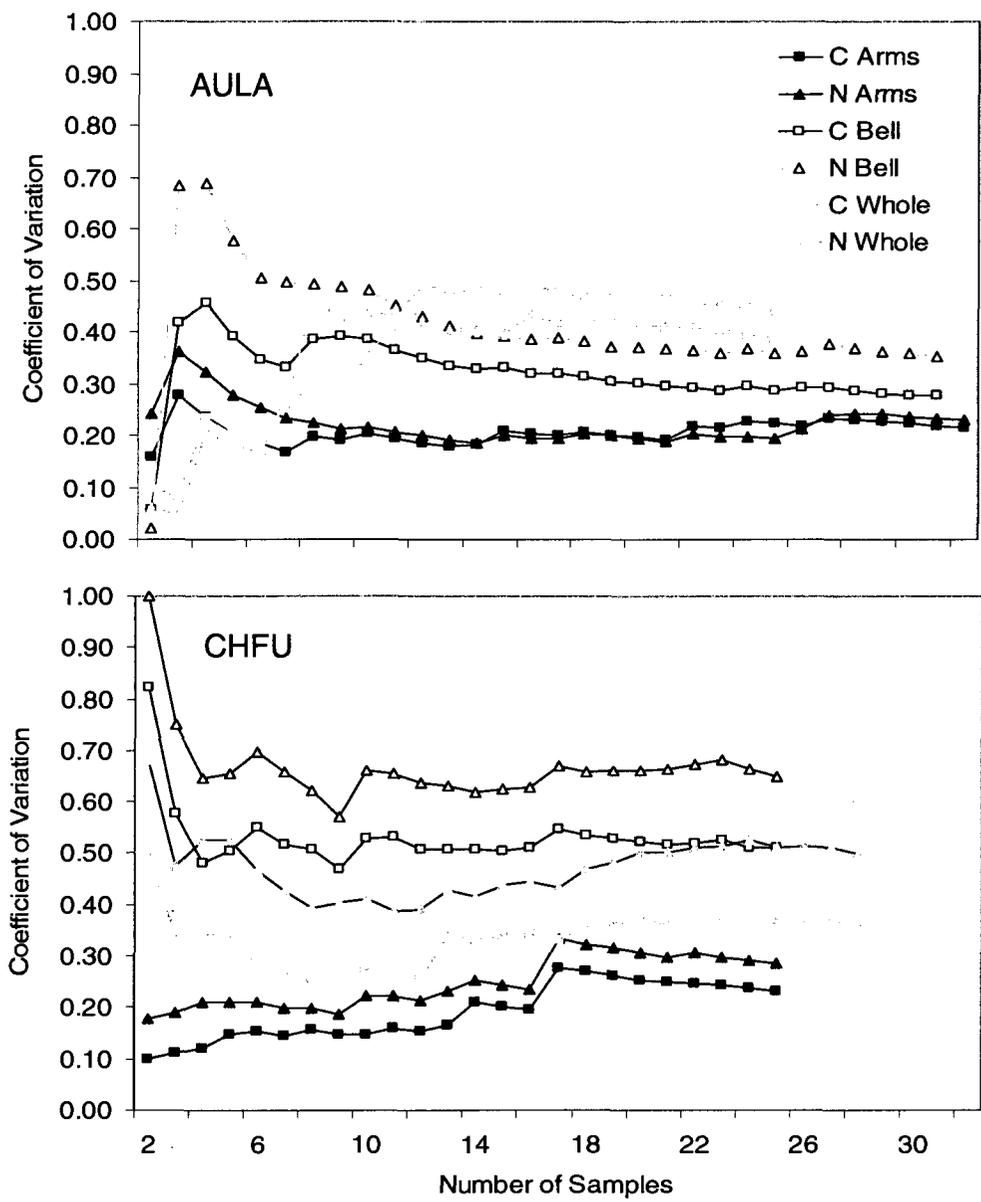
Fig. 6. Cumulative coefficient of variation (CV) of carbon (C) and nitrogen (N) in bell, oral arms/gonads, and whole *Aurelia* spp. (AULA; top) and *Chrysaora fuscescens* (CHFU; bottom) as an indicator of sample precision.
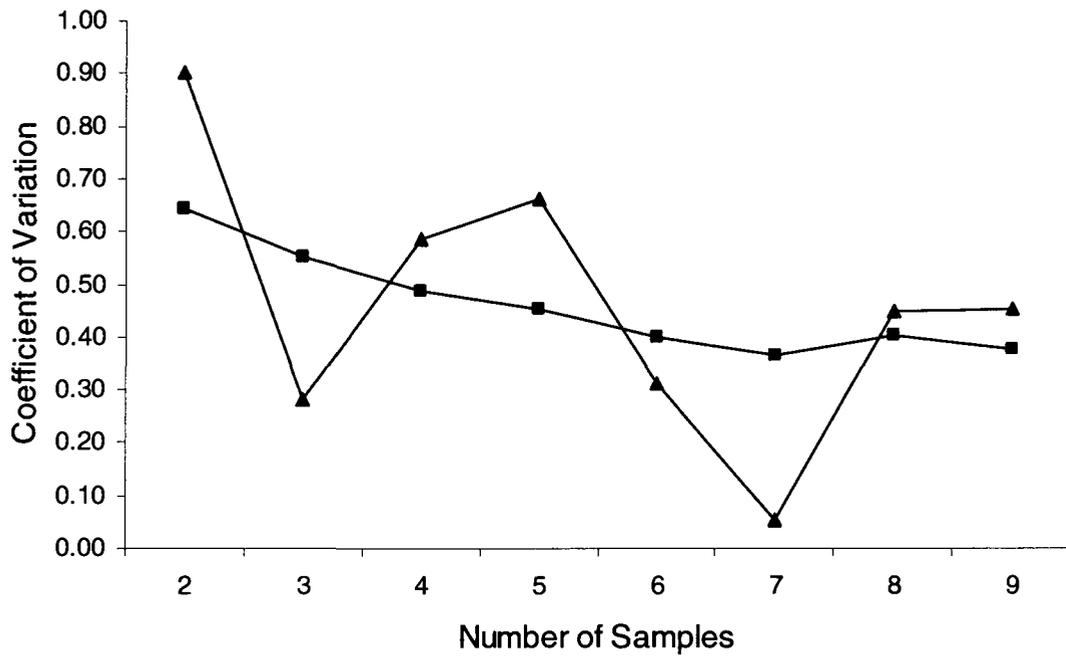
Fig. 7. Cumulative coefficient of variation of carbon (■) and nitrogen (▲) of *Phacellophora camtschatica* as an indicator of sample precision.

DISCUSSION

Species composition of jellies varied throughout the years of the study. The most abundant species for all years of the study combined was CHFU. In 2004, Monterey Bay was dominated by CHFU with moderate numbers of AULA. Yet in 2005, the species composition was almost exclusively PHCA and AULA. The following year, 2006, there were few scyphozoan jellies in the bay. In 2007, AULA and CHFU were once again abundant.

The scyphozoan jellies in this study exhibit complex life histories, with the larger medusa as the dominant stage. In temperate environments, production of medusae typically takes place in the spring (Purcell 2005), which is upwelling season off central California. Because 2006 was characterized by a late-onset, short-lived, upwelling season (Peterson et al. 2006), resources were likely insufficient to produce and/or mature medusae. Additionally, because of their short generation times (usually ≤ 1 yr), populations of jellies may respond to changes in environmental conditions with little time lag (Lynam et al. 2005). Thus, the interannual variability in abundance and species composition is likely a result of the intensity and timing of upwelling and subsequent productivity. No data were available on factors affecting reproduction during the benthic-polyp stage of Scyphozoan jellies off central California.

As predicted, jellies collected during upwelling, particularly CHFU, were smaller and less nutrient-rich than those collected during post-upwelling season.

The upwelling season occurs earlier in the year when animals are younger and have had less exposure to resources. By the later post-upwelling season, jellies had an opportunity to take advantage of abundant prey made available by nutrient-rich upwelled water, hence, they are more developed and mature. It is likely that AULA also is more C and N rich during post-upwelling season but a greater sample size is needed to detect it. Because the variability of C:N was minimal for AULA and CHFU, the lack of difference in C:N between seasons is likely not a factor of sample size. The lack of variation in C:N indicates both species maintain a relatively consistent ratio of carbohydrates to protein throughout the year.

The nutrient-rich species, CHCO, was least abundant and was collected in only one year. This species was not seen in large aggregated surface shoals like other scyphozoan species. Because net tows yielded so few CHCO, it was possible that they had a similarly sparse distribution at depth, which contributed to the small sample size. All individuals were collected within a three week period, so the small sample cannot be assumed representative of the size, distribution, or abundance of CHCO off central California. The low abundance of CHCO relative to other jelly species indicated that while it is more nutritionally beneficial than AULA, its lesser abundance likely makes them an insignificant portion of the diet of leatherback turtles. Despite the small sample, however, the nutritional data are important because there are no reported values of C and N for this species.

PHCA was only collected in 2005, inside Monterey Bay. A medusivore, PHCA preys upon *Aurelia* spp. (Strand & Hamner 1988, Widmer 2006). It is not surprising then, that PHCA was more nutrient-rich than its prey. PHCA did not have greater C or N content than CHFU or CHCO, which may indicate that it does not consume these species. PHCA are particularly fragile and seldom survived the net tow in good enough condition to be collected for nutritional analysis; therefore, it is likely that sample size was insufficient to detect a significant difference in nutritional value. As the most abundant scyphozoan species in 2005, a sufficient sample of bell diameters were collected to be representative of the size distribution at that time. Samples were limited to late summer from inside Monterey Bay, however, so additional study is needed to determine whether bell diameter is typical of the species during late summer months for central California. Again, the lesser relative abundance indicates that despite its moderate nutritional value, it is not likely consumed by foraging leatherbacks in significant numbers.

The most abundant species, CHFU, was more nutrient-rich than AULA. CHFU have oral arms which can extend more than 3-m past the bell (accessed 1 Apr 2009, www.montereybayaquarium.org), vastly different from the compact body plan of AULA that has oral arms that do not extend much past the bell margin. It would be useful to measure wet weight and volume of these species, whole and separated, to understand how the different structures factor into the foraging ecology of their predators. The greater nutritional value of CHFU,

coupled with its greater volume and longer oral arms may explain why leatherback turtles off central California are more often associated with CHFU (Benson et al. 2007a) and frequently consume only the oral arms and gonads of their prey.

The highly productive waters off central California yield more nutrient-rich *Aurelia* spp. and CHFU than the colder, less productive waters off the Pacific Northwest. Larson (1986) found 7.0% C and 2.0% N (DW) in one CHFU, and a mean of $4.3 \pm 0.4\%$ C and $1.3 \pm 0.1\%$ N (DW) in *Aurelia aurita* collected from April through November off British Columbia. The difference in C and N content may be inherent to the species, but because *Aurelia* spp. are similar enough to sometimes require genetic analysis to discern species (Gershwin 2001), it is more likely the difference in nutritional value was caused by conditions of the sampling locations. C:N values between 3.5 and 3.8 ± 0.1 have been reported for CHFU (Shenker 1985, Larson 1986). This indicates CHFU off central California have a greater proportion of carbohydrates to proteins than CHFU off the Pacific Northwest. Previous researchers had insufficient sample sizes to draw conclusions about CHFU populations off the Pacific Northwest and this is likely an additional source of variation from this study.

The degree of precision of C and N varied among species and whole and separated body components. The high degree of precision of the elemental analyzer indicates that the variability in the results was a reflection of the true

variation of C and N content among jellies, and not a function of measurement error. The C and N content of CHFU and AULA were greatly variable, but the stability of the cumulative CV indicated that variation was not an issue of sample size. Jellies analyzed were collected during post-upwelling and upwelling seasons, so the variability in nutritional value was likely a reflection of the productivity of the environment resulting in varying degrees of maturity of the jelly. The mean C and N values in PHCA and CHCO were both imprecise and greatly variable, so although the data were useful in providing new information on the value of PHCA and CHCO as prey for leatherback turtles in central California, it is clear that sample size of PHCA and CHCO was an insufficient representation of the population.

This study confirms the value of scyphozoan jellies as prey in the central California marine ecosystem and helps elucidate the foraging strategy of leatherback turtles. By foraging during late summer and early fall, leatherback turtles are taking advantage of scyphozoan jellies common to the surface waters of the area when they are most abundant, largest, and most nutrient-rich. Greater nutritional value in the oral arms and gonads of jellies provides an explanation for the observed selective foraging behaviour upon these portions of CHFU (J. Harvey & S. Benson, unpub. data). By limiting foraging efforts to the most nutrient-rich portion, leatherback turtles thus maximize their foraging success.

This study provided novel information about the ecology of scyphozoan jellies as prey for leatherback turtles off central California, but additional studies are needed to further characterize oceanographic conditions as they are associated with size, abundance, distribution, and nutritional value. An understanding of how C and N content varies in each species by wet weight and volume, and between oceanographic seasons among years may provide a link between leatherback turtle foraging and nesting success. Additional studies of lipid and caloric content of scyphozoan jellies would further elucidate the value of each species as prey for leatherback turtles. We also need to examine the absolute rather than relative abundance of jellies, and determine biomass and vertical and horizontal distribution throughout the water column. This may be possible with the development of acoustic sampling techniques that may be an important tool for resource managers in defining and characterizing critical foraging habitat (Ch. 2).

LITERATURE CITED

Benson SR, Forney KA, Harvey JT, Carretta JV, Dutton PH (2007) Abundance, distribution, and habitat of leatherback turtles (*Dermochelys coriacea*) off California, 1990-2003. Fish. Bull. 105:337-347.

Benson SR, Dutton PH, Hitipeuw C, Samber B, Bakarbessy J, Parker D (2007) Post-nesting migrations of leatherback turtles (*Dermochelys coriacea*) from Jamursba-Medi, Bird's Head Peninsula, Indonesia. Chelonian Conserv Biol 6:150-154.

Broenkow WW, Smethie WM (1978) Surface circulation and replacement of water in Monterey Bay. Est Coast Mar Sci 6:583-603.

Bugoni L, Krause L, Petry M, Maria V (2001) Marine debris and human impacts on sea turtles in Southern Brazil. Mar Pollut Bull 42:1330-1334.

Carr A (1967) So excellent a fishe. Natural History Press, Garden City, NY 248p.

Carr A (1987) Impact of nondegradable marine debris on the ecology and survival outlook of sea turtles. Mar Pollut Bull 18:352-356.

Dutton PH, Bowen BW, Owens DW, Barragan A, Davis SK (1999) Global phylogeography of the leatherback turtle (*Dermochelys coriacea*). J Zool Lond 248:397-409.

Dutton PH, Hitipeuw C, Zein M, Benson SR, Petro G, Pita J, Rei V, Ambio L, Bakarbessy J (2007) Status and genetic structure of nesting populations of leatherback turtles (*Dermochelys coriacea*) in the Western Pacific. Chelonian Conserv Biol 6:47-53.

Eckert KL, Luginbuhl C (1988) Death of a giant. Mar Turtle Newsl 43:2-3.

Eckert SA (1997) Distant fisheries implicated in the loss of the world's largest leatherback nesting population. Mar Turtle Newsl 78:2-7.

Eisenberg JF, Frazier J (1983) A leatherback turtle (*Dermochelys coriacea*) feeding in the wild. J Herpetol 17:81-82.

Frazier JG, Montero JLB (1990) Incidental capture of marine turtles by the swordfish fishery at San Antonio, Chile. Mar Turtle Newsl 49:8-13.

Gershwin L-A (2001) Systematics and Biogeography of the Jellyfish *Aurelia labiata* (Cnidaria: Scyphozoa). Biol Bull 201:104-119.

Holland DL, Davenport J, East J (1990) The fatty acid composition of the leatherback turtle *Dermochelys coriacea* and its jellyfish prey. J Mar Biol Ass U K 70:761-770.

James MC, Herman TB (2001) Feeding of *Dermochelys coriacea* on medusae in the Northwest Atlantic. Chelonian Conserv Biol 4:202-205.

Julian F, Beeson M (1998) Estimates of marine mammal, turtle, and seabird mortality for two California gillnet fisheries: 1990-1995. Fish. Bull. 96:274-284.

Larson RJ (1986) Water content, organic content, and carbon and nitrogen composition of medusae from the northeast Pacific. J Exp Mar Biol Ecol 99:107-120.

Limpus CJ (1995) Global overview of the status of marine turtles: a 1995 viewpoint. In: Bjorndal KA (ed) The biology and conservation of sea turtles (revised edition). Smithsonian Institute Press, Washington DC, p 605-609.

Lynam CP, Hay SJ, Brierley AS (2005) Jellyfish abundance and climatic variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries. J Mar Biol Ass U K 85:435-450.

Margaritoulis DN (1986) Captures and strandings of the leatherback sea turtle (*Dermochelys coriacea*) in Greece (1982-1984). J Herpetol 20:471-474.

National Marine Fisheries Service and U.S. Fish and Wildlife Service. (1998) Recovery plan for U.S. Pacific populations of the leatherback turtle (*Dermochelys coriacea*). National Marine Fisheries Service, Silver Spring, MD.

Peterson B, Emett R, Goericke R, Venrick E, Mantyla A, Bograd SJ, Schwing FB, Hewitt RP, Lo N, Watson W, Barlow J, Lowry M, Ralston S, Forney KA, Lavaniegos BE, Sydeman WJ, Hyrenbach D, Bradley RW, Warzybok P, Chavez FP, Hunter K, Benson S, Weise M, Harvey JT, Gaxiola-Castro G, Durazo R (2006) The state of the California current, 2005-2006, warm in the north, cool in the south. Report No. 47.

Pritchard PCH (1982) Nesting of the leatherback turtle, *Dermochelys coriacea* in Pacific Mexico, with a new estimate of the world population status. Copeia 4:741-747.

Purcell JE (2005) Climate effects on formation of jellyfish and ctenophore blooms: a review. J Mar Biol Ass U K 85:461-476.

Sarti L, Eckert SA, Garcia NT, Barragan AR (1996) Decline of the world's largest nesting assemblage of leatherback turtles. Mar Turtle Newsl 74:2-5.

Schneider G, Behrends G (1994) Population dynamics and the trophic role of Aurelia aurita medusae in the Kiel Bight and western Baltic. ICES J Mar Sci 51:359-367.

Schwing, FB, Murphree T, Green PM (2002) The Northern Oscillation Index (NOI): a new climate index for the northeast Pacific. Prog Oceanogr 53(2):115–139.

Shenker JM (1984) Scyphomedusae in surface waters near the Oregon Coast, May - August, 1981. Est Coast Shelf Sci 19:619-632.

Shenker JM (1985) Carbon content of the neritic scyphomedusae Chrysaora fuscescens. J Plankton Res 7:169-173.

Skillman RA, Balazs GH (1992) Leatherback turtle captured by ingestion of squid bait on swordfish longline. Fish. Bull. 90:807-808.

Skogsberg T, Phelps A (1946) Hydrography of Monterey Bay, California. Thermal Conditions, Part II. Proceedings of the American Philosophical Society 90:350-386.

Spotila JR, Reina RD, Steyermark AC, Plotkin PT, Paladino FV (2000) Pacific leatherback turtles face extinction: Fisheries can help avert the alarming decline in population of these ancient reptiles. Nature 405:529-530.

Starbird CH, Baldridge A, Harvey JT (1993) Seasonal occurrence of leatherback sea turtles (Dermochelys coriacea) in the Monterey Bay region, with notes on other sea turtles, 1986-1991. Calif Fish Game 79:54-62.

Stinson M (1984) Biology of sea turtles in San Diego Bay, California, and the north eastern Pacific Ocean. MS Thesis, San Diego State University, San Diego, CA.

Strand SW, Hamner WM (1988) Predatory behavior of Phacellophora camtschatica and size-selective predation upon Aurelia aurita (Scyphozoa: Cnidaria) in Saanich Inlet, British Columbia. Mar Biol 99:409-414.

Suwelo IS, Yusuf CY, Yamasaki K (1994) Leatherback turtles at Jamursba-Medi Beach, Kepala Burung, Irian Jaya. Mar Turtle Newsl 64:12.

Widmer CL (2006) Life cycle of *Phacellophora camtschatica* (Cnidaria: Scyphozoa). Invertebr Biol 125:83-90.

Work TM, Balazs GH (2002) Necropsy findings in sea turtles taken as bycatch in the North Pacific longline fishery. Fish. Bull. 100:876-880.

CHAPTER 2:

ACOUSTIC CHARACTERIZATION OF SCYPHOZOAN JELLIES AS PREY FOR LEATHERBACK SEA TURTLES *(DERMOCHELYS CORIACEA)* IN CENTRAL CALIFORNIA

Tanya R. Graham[1], James T. Harvey[1], Scott R. Benson[2], and David A. Demer[3]

[1]Moss Landing Marine Laboratories

8272 Moss Landing Road, Moss Landing, CA 95039

[2]Protected Resources Division

Southwest Fisheries Science Center

c/o MLML Norte

7544 Sandholdt Road, Moss Landing, CA 95039

[3]Advanced Survey Technologies Program

Southwest Fisheries Science Center

8604 La Jolla Shores Drive, La Jolla, CA 92037

ABSTRACT

Acoustic sampling techniques were developed to assess the abundance and distribution of scyphozoan jellies as prey for leatherback sea turtles (*Dermochelys coriacea*) foraging off central California. Five acoustic transects with corresponding net tows were selected where jellies were present and five where they were absent. Empirical bell-diameter-distribution data (26.2 ± 10.6 SD) were used to estimate target strength (*TS*) at 18, 38, 70, 120, and 200 kHz using a distorted-wave Born approximation scattering model. *TS* measurements of *in situ* animals at 38 and 200 kHz averaged -54.9 and -63.7 dB, compared with the model estimates of -61.9 and -70.5 dB re 1 m^2, respectively. Model estimates of *TS* at 18, 70, and 120 kHz were -53.9, -59.9, and -91.8 dB re 1 m^2, respectively. *TS* estimates of *in situ* jellies were not available at 18, 70, and 120 kHz. These *TS* estimates were used to develop an algorithm to extract jelly echoes from total acoustic backscatter. Echo integration methods applied in regions where tows contained jellies resulted in an estimate of mean numerical abundance (± SD) of 3217 ± 2276 jellies, with a mean density of 251 522 ± 57 504 jellies n.mi.$^{-2}$ and a mean concentration of 0.003 ± 0.002 jellies m^{-3}. The novel methods developed in this study can be used to characterize the distribution and abundance of scyphozoan prey for leatherback turtles in central California.

INTRODUCTION

To understand the foraging ecology of leatherback turtles off central California, we must examine the nutritional value and the distribution and abundance of scyphozoan jellies. Sparsely distributed jellies require more effort for turtle to obtain than jellies in large, dense aggregations over smaller spatial scales. It may be that central California offers nutrient-rich prey distributed in greater numbers over a smaller area than foraging grounds in other regions, thus making the trans-Pacific migration of leatherback turtles to central California (Dutton *et al.*, 1999; Benson *et al.*, 2007) energetically beneficial.

There is a paucity of information about the distribution of the four species of scyphozoan jellies common in central California (*Aurelia* spp., AULA; *Chrysaora colorata,* CHCO; *Chrysaora fuscescens,* CHFU; and *Phacellophora camtschatica*, PHCA), except that they are most common in retention areas. In northern Monterey Bay, biomass of *Chrysaora* sp. increases at a seasonally persistent front between cold water advected southward from the Año Nuevo upwelling center, into the warm waters retained nearshore (Graham *et al.*, 1992, 1997). Similarly, Benson *et al.* (2007) found scyphozoan jellies were common in surface waters ($\leq$ 1 m depth) in these areas from Pt. Reyes in the north to Monterey Bay in the south.

Traditional methods for sampling jellies are problematic. Historically, net samples have been used to assess their distribution and abundance. Although

useful in providing morphometric and taxonomic information, net tows are inherently problematic as they cannot resolve extreme small or large-scale patchiness commonly characteristic of jellies (Graham *et al.,* 2001). Large aggregations also can overwhelm and destroy a net (Brierley *et al.,* 2001), and fragile jelly tissues can be minced to unidentifiable pieces. Aerial observations can provide useful information about the surface distribution of jellies (Houghton *et al.,* 2006; Benson *et al.,* 2007) but cannot provide detailed morphometric data, nor do they offer any information about jellies at depth.

A multi-frequency echosounder is a powerful tool that can sample large volumes of water in a short period of time, and can provide estimates of vertical and horizontal distribution, biomass, and in some cases, taxonomic and morphometric information. It was traditionally thought that jellies were weak sound-scatterers because of their high water content (thus low density contrast with the surrounding water) so their contribution to total backscattered acoustic energy would likely be masked by other zooplankton. However, recent studies have indicated that though jellies scatter sound more weakly than zooplankton per unit biomass (Stanton *et al.,* 1996), they are typically large enough to scatter more sound per individual than most zooplankton at frequencies commonly used in scientific echosounders (Brierley *et al.,* 2001; Brierley *et al.,* 2005; Alvarez Colombo *et al.,* 2009).

As with any approach, acoustic sampling with an echosounder has some limitations. Traditionally deployed downward-looking echosounders are blind to the upper three to five meters of the water column where jellies are common (Benson *et al.*, 2007), and data must be validated by accompanying net tows. Also, the process of converting acoustic backscatter data into biologically relevant data requires an understanding of the sound-scattering characteristics of the target organism(s), particularly target strength (*TS*). *TS* is a measure of the portion of acoustic energy incident on an object that is scattered back towards the sound source and is a requisite parameter for estimating species abundance and biomass from acoustic survey data. However, sound scattering is a complex process which can make determination of *TS* for a particular species difficult. Among jellies, *TS* has been established for only a few species, including *Aurelia aurita* (Mutlu, 1996) and *Chrysaora hysoscella* (Brierley *et al.*, 2004; Table 1).

The methods most commonly used to determine *TS* of an organism are experiments on tethered animals, detections of *in situ* single targets, and the use of physics-based sound-scattering models. These methods are often used in a complementary, iterative approach to estimate *TS*. Experiments on tethered animals allow for precise knowledge of the target depth, orientation, and morphometrics. When conducted in a tank environment, confounding scatter from other organisms in the water column is no longer an issue. However, reverberation off the tank walls and the tether, and the near-field ranges of the transducer(s) and the animal need to be considered. Also, a tethered animal is

Table 1. Target strength (*TS*) estimates at various frequencies (kHz) from theoretical, laboratory, or field experiments on genera of jellies found off central California, including their species and bell diameter (cm).

Species	Size (cm)	Frequency (kHz)	*TS* (dB)	Source
		Hydrozoans		
Aequorea aequorea	7.4	18	-68.10	Brierley *et al.* (2001)
		38	-66.30	
		120	-68.50	
	6.5	18	-66.00	Brierley *et al.* (2004)
		38	-66.50	
		120	-71.50	
		200	-73.00	
	6.6	18	-68.20	Brierley *et al.* (2005)
		38	-66.70	
		120	-72.80	
Aequorea victoria	2.1-5.8	200-1000	-72.60	Monger *et al.* (1998)
		Scyphozoans		
Aurelia aurita	10.8	120	-76.40	Alvarez Colombo *et al.* (2009)
	9.5	120	-60.24	Mutlu (1996)
	15.5	120	-57.10	
	9.5	200	-64.27	
	11.5	200	-62.48	
	15.5	200	-56.47	
Aurelia autrans	8.0	38	-54.00	Nakken, in Mutlu (1996)
		38	-51.70	
	16.0	120	-54.20	
		120	-50.10	
Chrysaora hysoscella	26.8	18	-51.50	Brierley *et al.* (2001)
		38	-46.60	
		120	-50.10	
	41.0	18	-60.00	Brierley *et al.* (2004)
		38	-65.50	
		120	-68.00	
		200	-70.50	
	37.9	18	-53.40	Brierley *et al.* (2005)
		38	-49.00	
		120	-52.90	

not as free to move, flex, and change orientations as a free-swimming animal; and the acoustic incidence angle can modulate the *TS* of jellies by as much as a 10 dB (Monger *et al.*, 1998). Experiments with tethered jellies are laborious and also make it difficult to estimate *TS* for a range of sizes representative of the natural population. Measurements of individual free-swimming jellies in an *in situ* population can provide robust estimates of *TS*, but it is difficult to acoustically resolve individual animals, and then identify the species and size of the target. When targets are in close proximity to one another it is likely that overlapping echoes are perceived as a single stronger target, thus positively biasing *TS* estimates (Demer *et al.,* 1999). Net tows are used to verify the species composition of all possible scatterers and estimate their sizes. An additional challenge is then to link, perhaps in a statistical sense, the *TS* measurements to the animals caught.

Scattering models have become increasingly sophisticated and accurate (Stanton *et al.,* 1994, 1998) and can even account for the stochastic nature of sound scattering (Demer and Conti, 2003a, b). Models require input of critical parameters which include the size, shape, and orientation relative to the sound source, and ratios of density (*g*) and sound speed (*h*) of the animal and these parameters for the surrounding medium. Accuracy of many models, therefore, is limited by the accuracy of the model's parameters.

We developed acoustic methods to assess the distribution and abundance of jellies in the central California foraging area of leatherback turtles. The method was based on predictions of the distorted-wave Born approximation scattering model (DWBA; Chu *et al.*, 1993), validated with *in situ TS* estimates. Potential biases in each method were mediated and a reliable algorithm was developed to extract jelly echoes from total acoustic backscatter. These data enabled estimates of the abundance and distribution of potential scyphozoan prey of leatherback turtles.

METHODS

Cruises were conducted aboard the RV "John Martin". Acoustic data were sampled using a hull-mounted, multi-frequency (38 and 200 kHz), split-beam echosounder (Simrad EK60) and recorded via Ethernet to a laptop computer using ER60 software (Simrad AS, Version 2.1.1; Table 2). The echosounder system was calibrated before the study season using the standard sphere method (Johannesson and Mitson, 1983).

Table 2. Echosounder parameters used for all cruises. Transmitted power = 1000 W; transmitted pulse length = 1.024 ms; ping interval = 2.0 sec; and TVG range correction offset = 2 samples.

	2005		2007	
Frequency (kHz)	38	200	38	200
Two-way beam angle (dB re 1 Steradian)	-15.5	-20.7	-15.5	-20.7
Transducer gain (dB)	19.71	20.78	19.34	20.70
Sa correction (dB)	-0.72	-0.34	-0.71	-0.29
Minor axis 3dB beam angle (degrees)	12.66	7.09	11.93	6.72
Major axis 3dB beam angle (degrees)	11.87	6.90	11.70	6.76

The cruise dates (Figure 1), study area, and net-sampling methods are described in detail in Chapter 1. Before each net tow, a CTD (Sea-Bird SBE19) was used to collect conductivity, temperature, and pressure data to a depth of 100-m or, when shallower, to 10-m from the bottom.

	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
2003	●		●	●	●	●	●	●	●
2004	●		●		● ●	● ■	●	● ■	●
2005	●		●	●	●	● ■	●	● ■■	●
2006		●	●	●	●	● ■	● ■	●	●
2007	●	●		● ■	●	■	■	● ■	
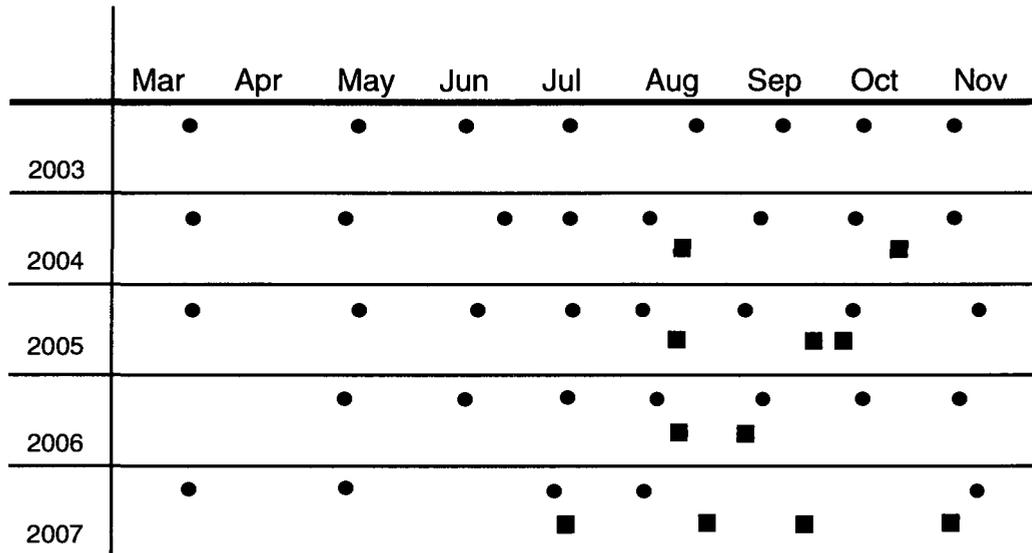
Figure 1. A record of cruise effort aboard the RV "John Martin". Horizontal position of marker indicates approximate date of the cruise within the month noted. (●) Center for Integrated Marine Technologies (CIMT) cruises, (■) Moss Landing Marine Laboratories (MLML) cruises.

To obtain the best fit from the DWBA scattering model input parameters appropriate for scyphozoan jellies were selected. To develop a more comprehensive model, bell diameter data presented in Chapter 1 were combined with additional bell diameter data from tows conducted aboard the RV "David Starr Jordan" collected from 31 Aug through 15 Sept 2008 (Figure 2).
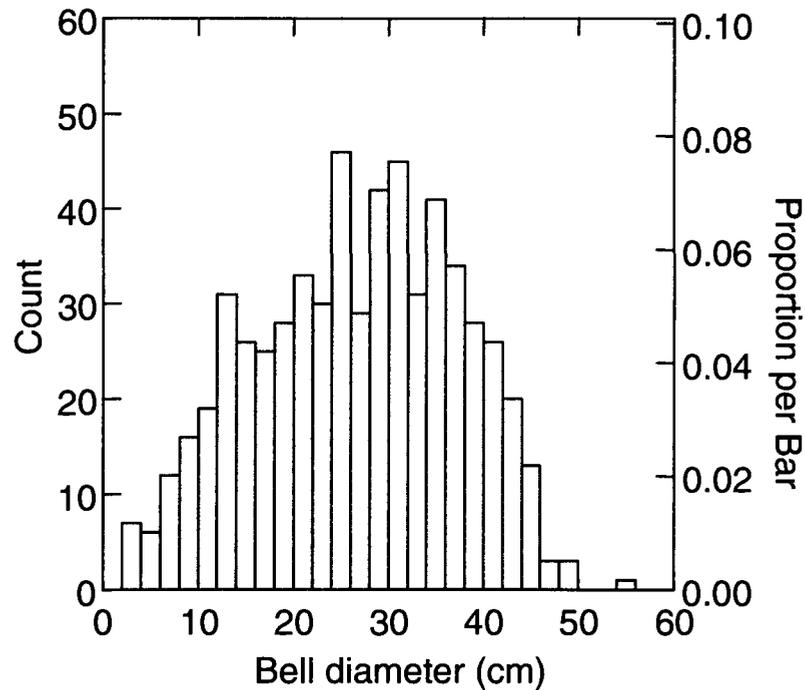
Figure 2. Distribution of jelly bell diameter (D; cm) which was used as an input parameter in the DWBA model. This distribution includes data from Chapter 1 and additional data from a cruise aboard RV "David Starr Jordan"; mean D = 26.2; SD = ± 10.6 cm, n = 595.

DWBA model parameter values of g and h were taken from Warren and Smith (2007), and were the only measures available for scyphozoan jellies. Ratios of the bell heights and radii in the relaxed and contracted swimming positions of the jelly were input as suggested by Monger *et al.* (1998; Figure 3). *TS* was calculated over a range of frequencies (18, 38, 70, 120, and 200 kHz) and distributions of inferred incident angles (detail below) and observed bell diameters. All *TS* values are presented in dB re 1 m^2. As jellies exhibit radial symmetry, only angles of incidence from 0° to 90° were considered.

	DWBA input
g	1.009
h	1.0004
$b_1{:}a_1$	1.31
$b_2{:}a_2$	0.90
$a_2{:}a_1$	1.00
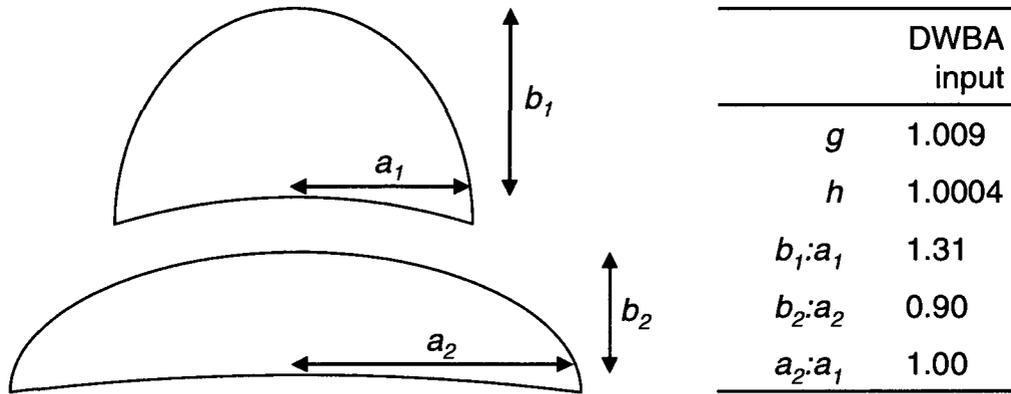
Figure 3. Parameters incorporated in the DWBA model included sound speed (c = 1500 m s^{-1}), density (g) and sound speed (h) contrast, and height:radius and radius:radius ratios for a jelly with a relaxed- and contracted-bell (figure recreated from Monger et al., 1998).

To calculate expected distributions of TS versus acoustic frequency, the distribution of sound incidence angles first needed to be estimated. Angles occurring in natural populations were unknown; therefore, the distribution of angles was estimated by minimizing the root-mean-square error between the modelled TS and the published TS estimates for scyphozoan jellies. Values of reduced TS (TS_{re}),

$$TS_{re} = TS - 20\log 10(D),\qquad(1)$$

were plotted versus the product of the acoustic wavenumber (k; m^{-1}) and the bell diameter (D; m),

$$kD = \frac{2\pi}{\lambda} \cdot D,\qquad(2)$$

where λ (m) is the acoustic wavelength. This allows *TS* of jellies of various sizes to be compared as a function only of frequency. A second order polynomial was then fitted to the plot, using the least-squares method. For each TS_{re} value on the polynomial function, the model data was searched to find the *kD* that corresponded most closely to the *kD* value from published data. Model *kD* values were then used to create a distribution of angles at which TS_{re} values best matched published TS_{re} values. Mean *TS* was then calculated as a function of frequency for every value in the empirical bell diameter distribution at the mean incident angle and within $\pm$ one SD (80.6 $\pm$ 1.0 °).

Segments of acoustic data selected for analysis corresponded to five locations at which jellies were present in net tows, and five at which they were absent (Figure 4). No data from 2006 were used as net tows failed to collect jellies that year. Data were post-processed in SonarData Echoview software (v. 4.6) with an applied threshold of -75 dB (S_v). Sound speed (*c*) and absorption coefficient (α; Francois and Garrison, 1982) were calculated specific to each sampling location using salinity and temperature values at the thermocline as indicated by CTD data (Table 3). In each echogram, analysis regions were defined for the duration of the tow, from 4-m to the maximum tow depth. Data above 4-m depth were within the acoustic transmit pulse and near field and were excluded from all analyses. If the bottom return was missing at either frequency, the pings affected were defined as bad data and excluded from the analyses.

43
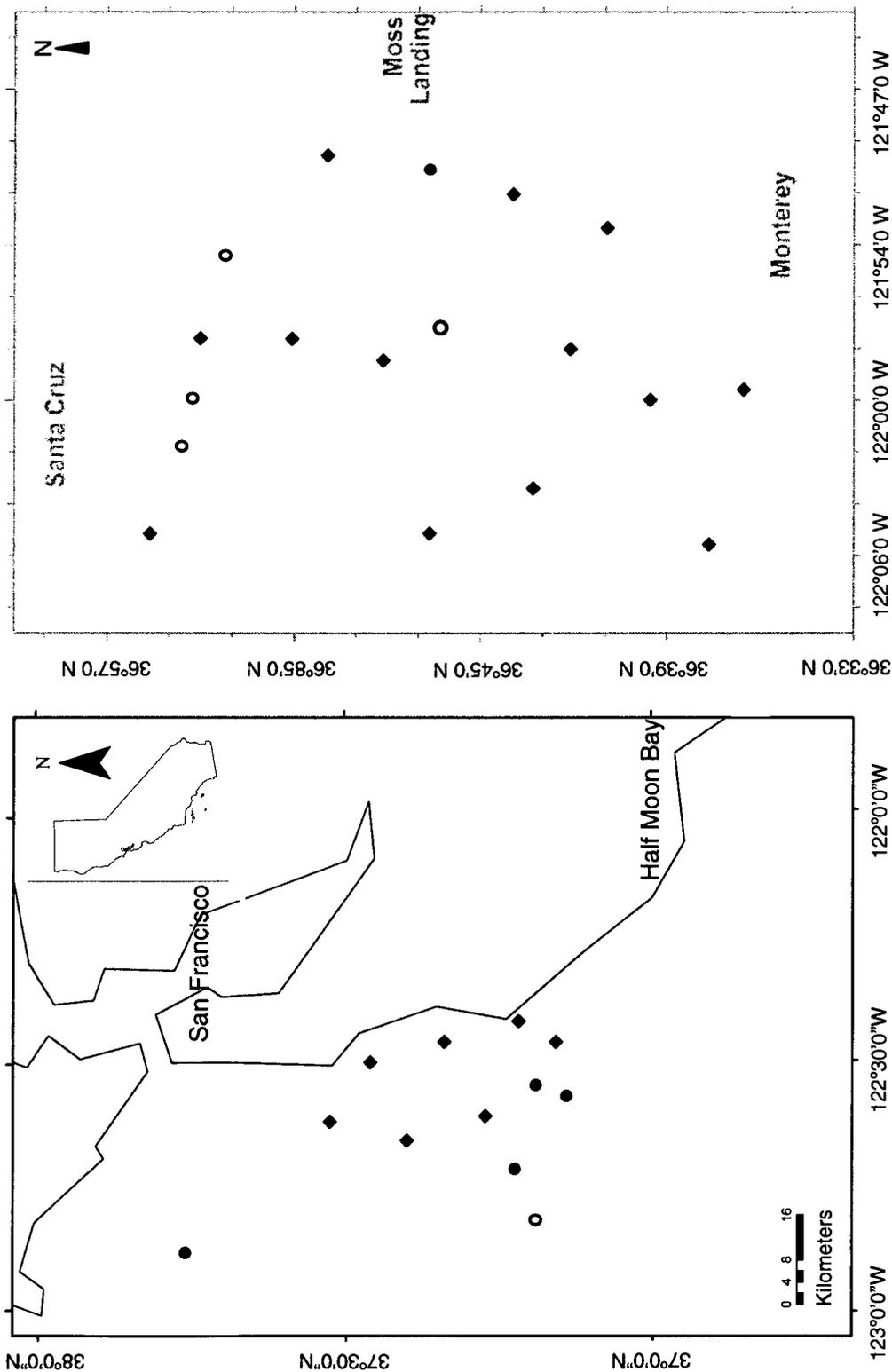
Figure 4. All net tow and acoustic sampling locations off central California. Locations selected for additional analysis of accompanying acoustic data when jellies were present (●), or absent (O); all other tow locations (◆).

Table 3. Cruise date, sound speed (c) and absorption coefficient (a) at frequencies of 38 and 200 kHz for each tow region. (*) denotes presence of jellies in net tow.

Date	c (m/s)	a-38 kHz (dB/km)	a-200 kHz (dB/km)
*15 Aug 2005	1 497.2	9.3	57.0
16 Aug 2005	1 495.5	9.3	56.7
*29 Sep 2005	1 500.0	9.1	59.8
29 Sep 2005	1 493.8	9.4	54.8
*30 Sep 2005	1 497.0	9.2	57.6
*2 Oct 2005	1 497.6	9.2	57.7
12 Jul 2007	1 494.9	9.5	56.4
24 Aug 2007	1 493.6	9.5	55.0
24 Aug 2007	1 495.5	9.6	56.9
*30 Sep 2007	1 497.6	9.3	57.8

To calculate TS of in situ animals, virtual echograms of single targets were created in Echoview (split-beam, method-one algorithm; Figure 5). Threshold values were applied to minimize the inclusion of weak scatters and noise. The minimum threshold was set at -80 dB for targets at 38 kHz, and at -85 dB for targets at 200 kHz (Alvarez Colombo et al., 2009). Because the signal-to-noise ratio for weakly-scattering targets is progressively reduced with increasing angle from the acoustic axis, the estimates of TS for single targets are increasingly positively biased versus increased off-axis angle (Fleischman and Burwen, 2000; Figure 6). Additionally, increased range from the transducer results in a lower signal-to-noise ratio and an increased insonified volume, thus increasing the likelihood of positive bias from multiple scatterers being perceived as a single target (Demer et al., 1999). Both sources of bias were evident at 200 kHz, thus

data at that frequency were limited to ≤ 2° off-axis and ≤ 10 m depth (Figure 7).

Modelled and measured *TS* estimates were compared with literature values

using *TS*$_{re}$ versus *kD* as previously described.
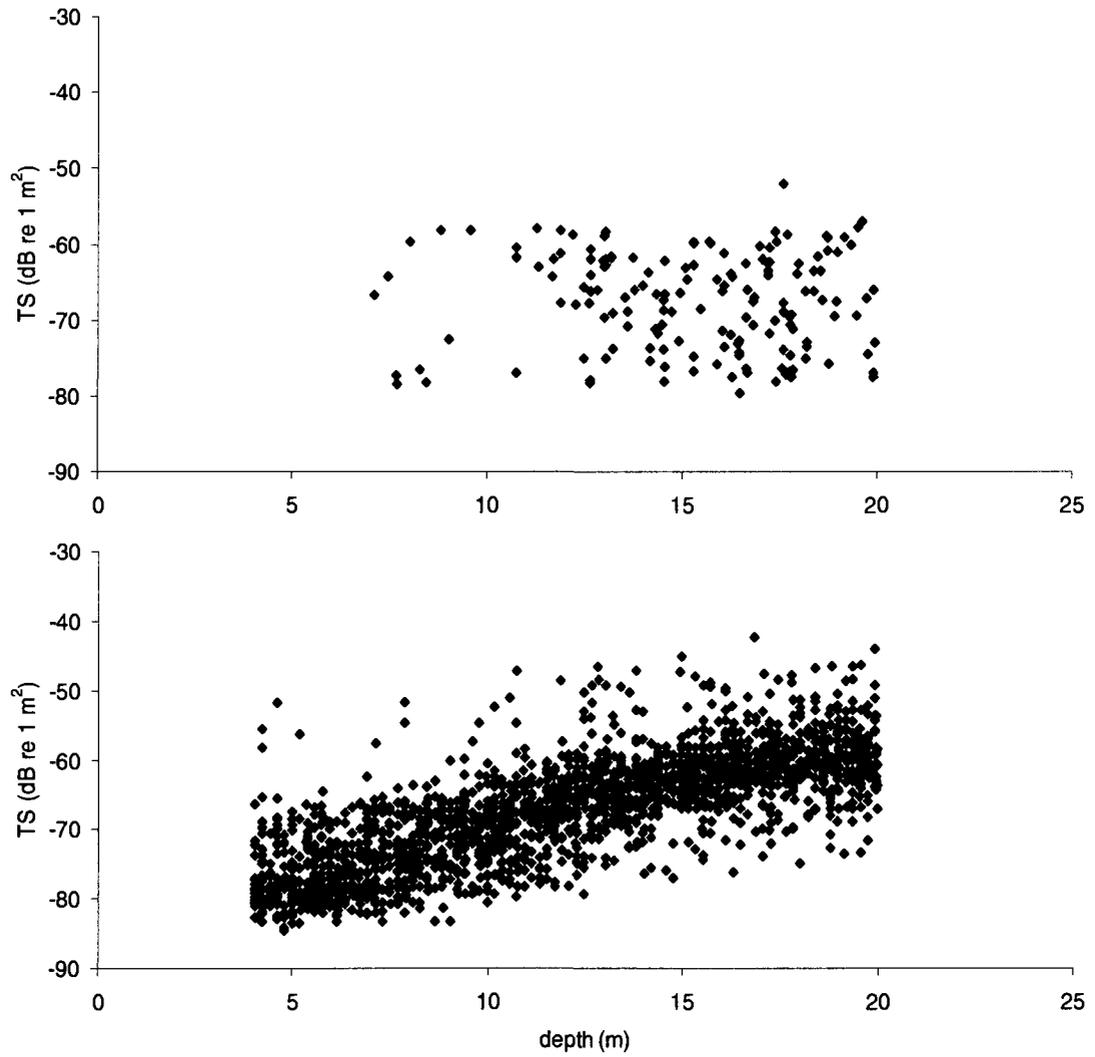
Figure 5. *TS* (dB re 1 m^2) of all targets detected greater than 4 m and less than 20 m depth at 38 kHz (top) and 200 kHz (bottom) by depth (m).
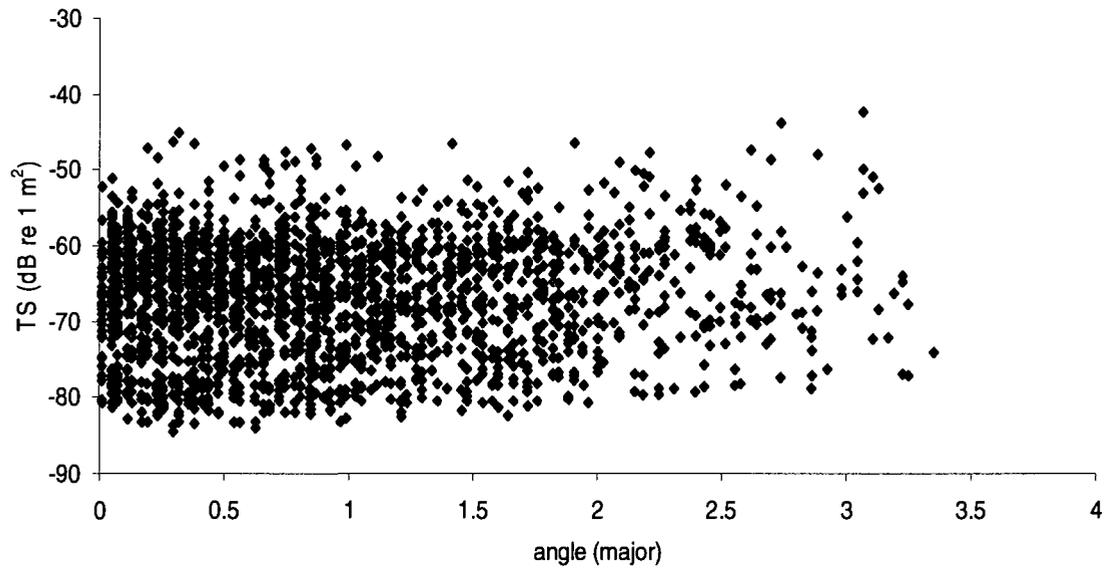
Figure 6. *TS* (dB re 1 m^2) of all targets detected at 200 kHz versus angle (degree) off the major beam axis.
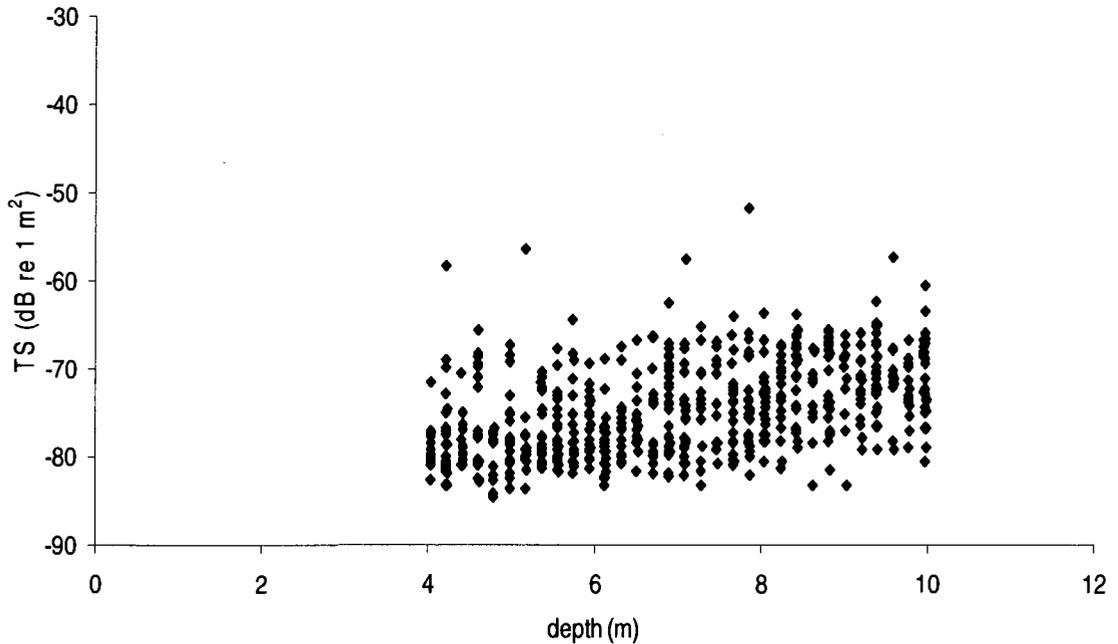
Figure 7. *TS* (dB re 1 m^2) of targets detected at 200 kHz restricted in depth (4 to 10 m) and off-axis angle ($\leq$ 2 °) to reduce positive bias associated with the range from the transducer and possible false detection of multiple targets as a single target.

Results of the DWBA model were used to develop an algorithm to enable echo integration methods to estimate the abundance and density of jellies (Figure 8). The algorithm exploits differences in S_v (volume backscattering strength, dB re 1 m^{-1}) at two frequencies (Greenlaw and Johnson, 1983) using masks to reject backscatter that does not match the criteria established by the DWBA model. The 200 and 38 kHz echograms were each dilated with 7x7 convolutions to reduce stochastic variations. Then, based upon the range between the upper and lower error bounds (± SD) of modelled TS at 200 kHz minus TS at 38 kHz, the S_v were considered to be jellies if their S_v-differences were between -15 and -4 dB (Figure 8). A Boolean mask was then applied to the original 38 kHz S_v data, to reject all Sv outside of the S_v-difference range. After applying this jelly detection algorithm, the resulting 38 kHz S_v echogram contained only data from putative jellies.

Within the processed 38 kHz echograms, analysis regions were defined by the depth, time, and locations of the net tows. S_v data from the defined region were integrated and mean backscattering cross section ($\sigma_{bs} = 10^{TS/10}$; m^2) was calculated from *TS* measurements of *in situ* targets. Areal density, numerical abundance, and volume density were calculated as follows (Alvarez Colombo *et al.*, 2009):

$$\rho_A = \overline{s_A} / (4\pi \cdot \overline{\sigma_{bs}}) \qquad (3)$$

$$n_{total} = \rho_A \cdot A \qquad (4)$$

$$\rho_V = \overline{s_v} / \overline{\sigma_{bs}} \qquad (5)$$

where ρ_A is the areal density (jellies n.mi.$^{-2}$); $\overline{s_A}$ is the mean nautical area

backscattering coefficient (NASC; m^2 n.mi.$^{-2}$); $\overline{\sigma_{bs}}$ is the mean backscattering

cross section of jellies (m^2); n_{total} is the numerical abundance of jellies; A is the

area surveyed (n.mi.^{2}); ρ_V is the volume density (jellies m^{-3}); and $\overline{s_v}$ is the mean

volume-backscattering coefficient (m^{-1}).
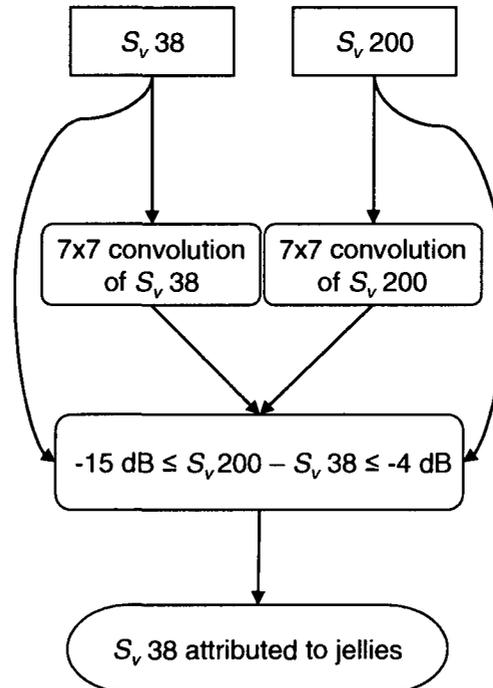
Figure 8. Algorithm to extract echoes of jellies from multi-frequency volume-backscatter data. A Boolean mask, defined by the differences in S_V at 200 and 38 kHz, is used to identify echoes from jellies.

RESULTS

Net tows selected for analysis of corresponding acoustic data contained

four species of scyphozoan jelly— AULA, CHCO, CHFU, and PHCA (Table 4).

Mean bell diameter of jellies from corresponding tows was 33.4 ± 8.1 cm (n =

42).

Table 4. Mean bell diameter (cm), standard deviation (SD), and species
composition (n = number sampled) of jellies collected in net tows from regions
selected for analysis of acoustic data. PHCA = *Phacellophora camtschatica*;
CHFU = *Chrysaora fuscescens*; CHCO = *Chrysaora colorata*; AULA = *Aurelia*
spp.

Date	Species (n)	Mean	SD
15 Aug 2005	PHCA (3)	30.0	2.8
29 Sep 2005	CHFU (4), PHCA (1)	30.2	14.1
30 Sep 2005	CHFU (5)	37.0	4.2
2 Oct 2005	CHFU (6), CHCO (1)	33.6	6.4
30 Sep 2007	AULA (18), CHFU (4)	30.2	6.9

Mean *TS* of *in situ* targets and *TS* predicted by the DWBA model were

similar (Figure 9). At 38 kHz, mean *TS* of *in situ* targets (-63.7 dB) was less than

the model estimate (-54.9 dB) but was within the error bounds; whereas at 200

kHz, *TS* of *in situ* targets (-70.5 dB) was less than the minimum predicted by the

model (-64.0 dB). The DWBA model estimated mean *TS* of -53.9 dB at 18 kHz, -

59.9 dB at 70 kHz, and -61.8 dB at 120 kHz dB.
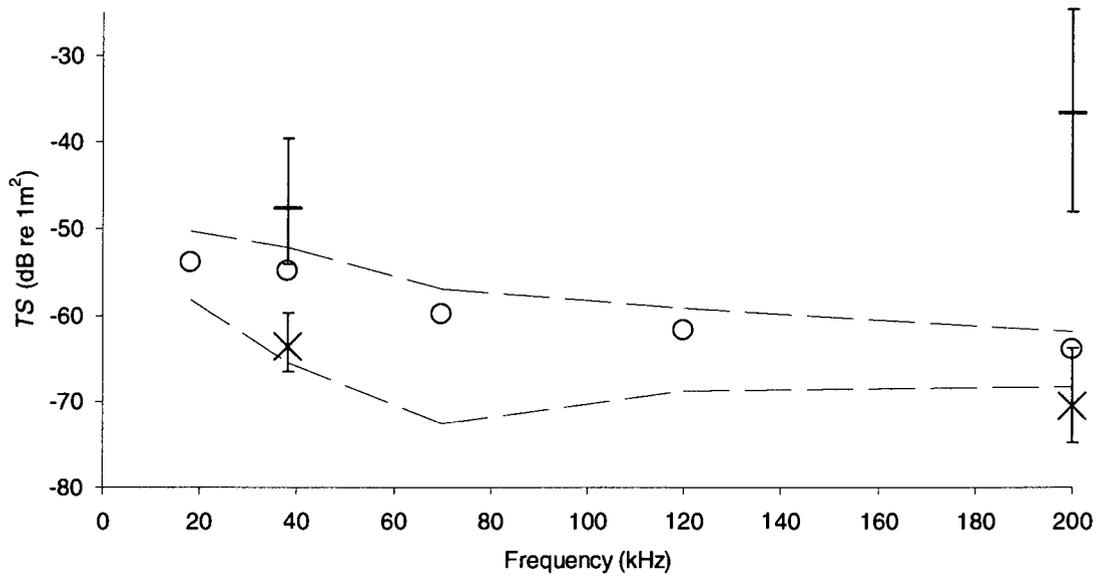
Figure 9. Mean *TS* values (dB re 1 m^2) by frequency (kHz) estimated from the DWBA model (O) ± one SD (--) and *TS* from detected *in situ* single targets when jellies were present (**X**) and absent (—) ± one SD.

Available estimates of *TS* at 38 kHz for scyphozoan jellies varied more than 18 dB (-65.5 to -46.6 dB), and the animal sizes also varied greatly (8 to 41 cm) which makes direct comparison of *TS* estimates difficult. When *TS*$_{re}$ were compared, however, the results from the DWBA model and the *TS* estimates of *in situ* targets matched the literature well, particularly values for *C. hysoscella* (Brierley *et al.,* 2004) and recent estimates for *Aurelia* spp. (Alvarez Colombo *et al.,* 2009; Figure 10).
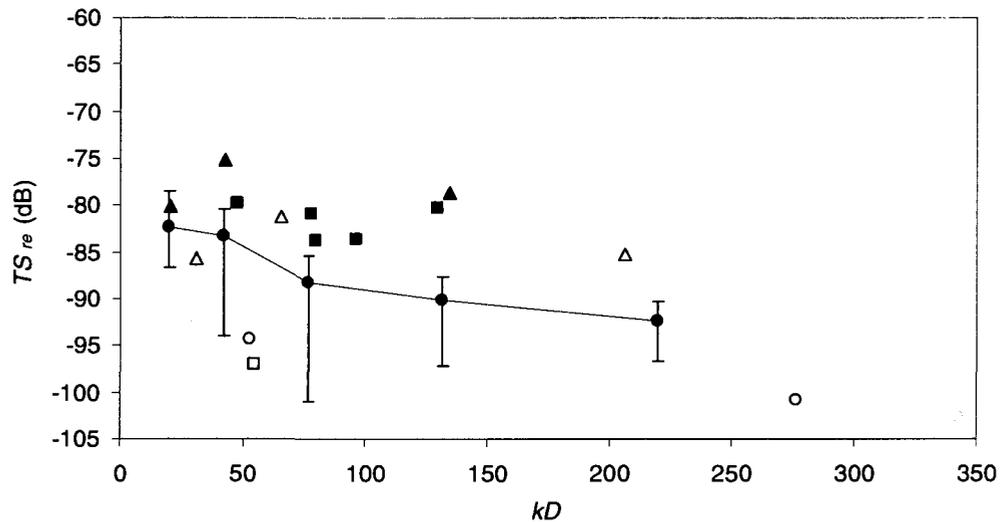
Figure 10. Summary of reduced target strength (TS_{re}; dB) versus the product of the acoustic wave number and the bell diameter (kD) for jellies measured in this and other studies. (-•-) DWBA ± SD; and (O) *in situ* this study; (■) *Aurelia aurita* (Mutlu, 1996); ( ) *Aurelia autrans* (Nakken cited in Mutlu 1996); (□) *Aurelia* spp. (Alvarez Colombo *et al.*, 2009); (▲) *Chrysaora hysoscella* (Brierley *et al.*, 2001); ( ) *C. hysoscella* (Brierley *et al.*, 2004); (△) *C. hysoscella* (Brierley *et al.*, 2005).

The 38 kHz S_v data corresponding to tows containing jellies indicated a weakly-scattering layer of varying density, sometimes overwhelmed by a dense layer apparent in the S_v with 200 kHz (Figure 11). The layer visible with 38 kHz was typically situated just above the dense layer using 200 kHz. No such layer was visible using 38 kHz, but the dense layer was present using 200 kHz, when there were no jellies in the tows (Figure 12).

The jelly algorithm was effective at removing sources of scatter not likely to be from jellies. When applied, the 38 kHz echograms retained scatter from the diffuse 38 kHz S_v layer, whereas the denser scattering layer at 200 kHz was nearly completely removed (Figure 12). Echo-integration analysis of the

52
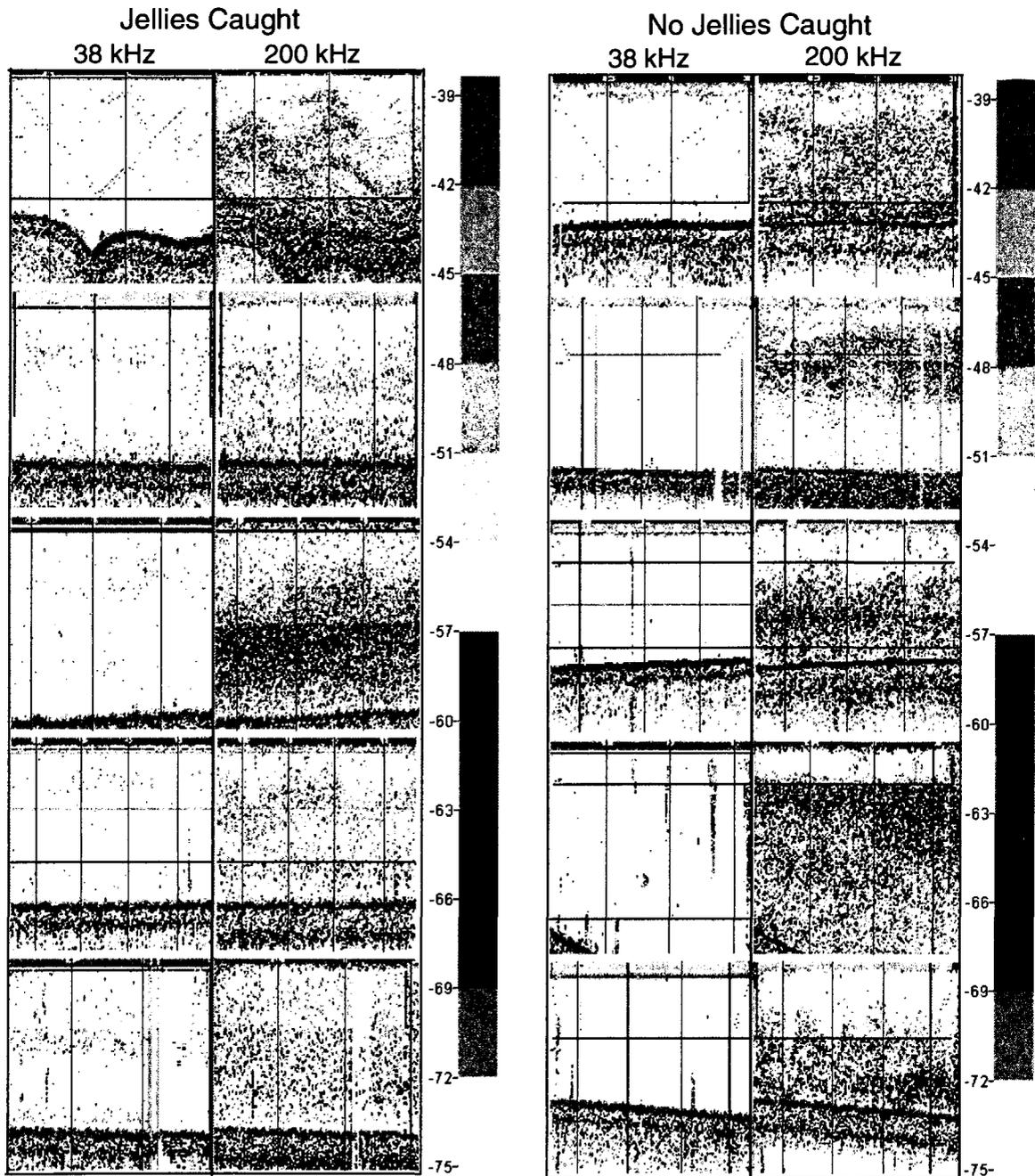
Figure 11. Paired raw echograms corresponding to tows with jellies in the catch (left panel) and tows when no jellies were collected (right panel) at 38 kHz (left side of pair) and 200 kHz (right side of pair). The analysis regions are highlighted in pale yellow. Vertical lines indicate 0.25 n.mi. increments. Echograms are in chronological order from top to bottom. V- or U -shaped lines visible in some echograms represent the approximate path of the net tow.
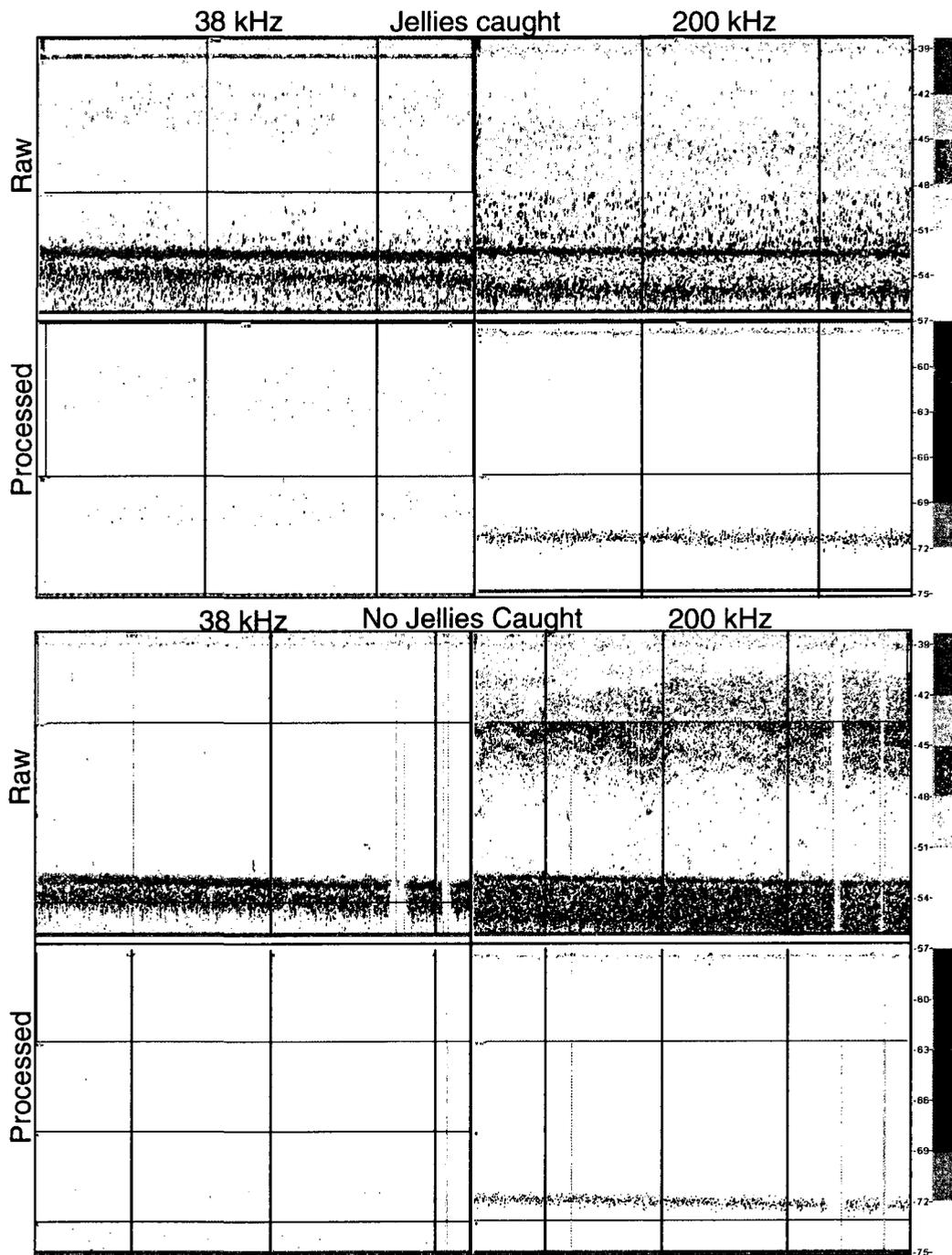
Figure 12. Raw (top row of panel) and processed (bottom row of panel) echograms using 38 kHz (left) and 200 kHz (right) for regions where jellies were (top panel) and were not caught (bottom panel). Vertical lines indicate 0.25 n.mi. increments. Vertical purple bands were regions of poor data and were not included in the analysis region (pale yellow).

regions where tows contained jellies indicated a mean areal density of 251 522 ±

57 504 jellies n.mi.$^{-2}$, a volume density of 0.003 ± 0.002 jellies m^{-3}, and a mean of

3217 ± 2276 jellies (Table 5). The mean number of jellies was greater in these

regions than in regions where no jellies were collected in tows. The difference,

while marginally significant (two-sample t-test, a = 0.05, P = 0.06), supports the

validity of the algorithm as no difference would have been expected if the

algorithm failed to extract backscatter from jellies.

Table 5. Mean (± SD) areal density (ρ_A; jellies n.mi.$^{-2}$), numerical abundance
(n_{total}) and volume density (ρ_V; jellies m^{-3}) of jellies from scatter at 38 kHz after
application of the algorithm to regions where jellies were present in, or absent
from the net tow catch.

	Present		Absent	
	Mean	SD	Mean	SD
ρ_A	251 522	57 504	148 231	169 378
n_{total}	3 217	2 276	816	859
ρ_V	0.003	0.002	0.003	0.004

DISCUSSION

The *TS* estimates from the DWBA model compared well with the *TS*

measured from *in situ* targets and *TS* values available from other sources, but

the model could be improved through use of more accurate parameters, and the

use of the SDWBA model for large angles of incidence. The values for *g* and *h*

from Warren and Smith (2007) are for small jellies (2 to 11 cm) of a species

uncommon to the study area (*Cyanea capillata*). Warren and Smith (2007) were

only able to obtain a single estimate of *h*, so the accuracy and precision of the

measure are unknown. Model accuracy would be increased with estimates of

the distributions of *g* and *h* specific to the scyphozoan jellies in the study area.

Also, because the SDWBA model is a better predictor of *TS* than the DWBA

model at incidence angles away from the main scattering lobe (Demer and Conti,

2003a), the SDWBA model may provide more accurate results, particularly for

higher acoustic frequencies and greater animal tilts.

Additionally, video observations of *in situ* jellies, using a stereo camera

equipped with pitch and roll sensors would provide estimates of the distributions

of jelly orientation and acoustic incidence angles, and changes in bell dimensions

with swimming motion that would allow for accurate and precise modeling of *TS*

for a particular species of jelly.

Even if input parameters are accurate, the DWBA scattering model may

have underestimated *TS* because it did not incorporate sound scattering from the

oral arms of the jelly. *Aurelia* spp., however, have relatively short oral arms that do not extend much past the bell margin, so the contribution of their oral arms to the backscatter may be insignificant and the model accurate. In contrast, species such as *C. fuscescens* can have thick robes of oral arms that can extend in length up to six-times the measure of the bell diameter (estimated at more than 3-m beyond the bell for this study; A. Morandini, unpub. data), that are likely to be significant sources of scatter. Until the contribution of scatter from the oral arms can be included, models may be best suited to species such as *Aurelia* spp. where the contribution from oral arms is unlikely to be significant.

TS estimates of *in situ* targets in this study were more comparable with data available from other sources than the model results; however, there are potential sources of bias that must be considered. Increased numerical density in some areas may positively bias *TS* estimates of *in situ* targets as multiple targets may be falsely interpreted as larger single targets. By restricting acceptance of single targets to those detected on consecutive pings over multiple frequencies, the positive bias can be reduced (Demer *et al.*, 1999). Optimally, this method employs a knowledge of the relative transducer geometries (pitch, roll, yaw, *x*, *y*, and *z*), which was not estimated for this study.

Available *TS* estimates of scyphozoan jellies vary as much as -20 dB. Only Alvarez Colombo *et al.* (2009) explicitly considered positive bias associated with increasing off-axis angle. Their estimate at 120 kHz (-76.4 dB) was

approximately four fold less than the TS at 200 kHz from this study (-70.5 dB), though the jellies in their study were substantially smaller (10.8 cm versus 33.4 cm). When TS_{re} was plotted versus kD (Figure 10), however, their estimate (-97.07 dB) was comparable with the measurements in this study (-94.28 and -100.90).

These model and *in situ* TS estimates do not explicitly consider the effect of changing body condition (such as gravid or full stomach) or the effect of mixed-species populations on TS estimates. *Aurelia* spp. exhibit considerable variation in size of medusae at maturity (Lucas, 2001) and have brood pouches that can be densely packed with planulae (Lucas and Lawes, 1998). Additionally, when food resources are limited, maturity is obtained at smaller sizes (Ishii and Båmstedt, 1988), thus the assumption that smaller animals will result in lower TS may not always be valid. TS estimates of *in situ* animals inherently incorporate this potential variability, yet to more accurately apportion echo-integration values to jellies, TS measures for gravid/non-gravid or starved/satiated individuals must be paired with knowledge of the proportion of each within the study area. This is similarly true for accurate apportioning of echo-integration values to each species when sampling mixed-species groups of jellies.

After the algorithm was applied to regions where tows did not contain jellies, some scatter remained, so other sources of scatter must be considered.

Parasites such as hyperiid amphipods and small fish often associated with jellies do not significantly contribute to scatter at 38 kHz (Alvarez Colombo *et al.,* 2003; Brierley *et al.,* 2004), so they are unlikely sources for the remaining scatter. It is more likely that net tows were simply ineffective at catching all jellies, particularly when density was minimal. The net used in the study was designed to sample zooplankton, so the pressure wave created by the net may have pushed some jellies out of the path. Moreover, when jellies were caught in the net, they were frequently destroyed in the cod end, so estimates of size and species were impossible to discern at times. Also, at the onset of this study, nets were towed through strong layers visible using 200 kHz. After this study was completed, tows with a newly acquired midwater-trawl net were set through layers appearing more prominently at 38 kHz, and these tows were nearly always successful at collecting identifiable jellies. Tows without jellies presented in this study are more likely representative of lesser densities of jellies and sampling difficulty rather than a total absence of jellies.

The validity of the jelly-classification algorithm is supported by the similarity of the layer to those previously described. The jellies appeared as continuous layers of varying density, typically at 10 to 30 m depth, consistent with layers described for *Aurelia* spp. (Alvarez Colombo *et al.,* 2009). The echogram for 30 Sep 2007 (bottom left in Figure 11), indicated an additional continuous layer just above the seafloor, similar in appearance to layers attributed to the scyphozoan jelly *Lychnorhiza lucerna* (Alvarez Colombo *et al.,* 2003). Though *L.*

lucerna is not found in the study area, it is possible that other scyphozoan species exhibit similar distributional patterns. Bottom trawls or video observations would be required to confirm the scattering layer near the seafloor as comprised of jellies.

The numerical abundance calculated from echo integration is somewhat surprising given how few jellies were collected in tows, but the data are strongly supported by aerial observations of jellies (Benson *et al.*, 2007). If surface abundance and distribution are indicative of what occurs at depth, then the number estimated by the acoustic analysis is supported and validates the ineffective nature of tows for abundance estimates of jellies. Furthermore, traditionally-deployed, downward-projecting echosounders cannot resolve targets in the upper 4 or 5 m of the water column, so numerical abundance is likely an underestimate.

Additional work needs to be conducted to fully characterize the leatherback turtle foraging area off central California. Accurate *TS* estimates and wet-weight measures for each species would enable biomass to be calculated from echo-integration values and be apportioned to species. The development of side-looking acoustic techniques would provide information about jellies in surface waters (i.e. in the unsampled regions between the surface and the transducer, and within the transmit pulse and nearfield for traditionally-deployed echosounders). Leatherback turtles are more closely associated with *C.*

fuscescens than other species (Benson *et al.,* 2007), so the ability to detect and identify jelly species within acoustic backscatter data may be critical for assessing foraging habitat.

The frequency-specific scattering characteristics of jellies make acoustic assessments of their distribution and abundance in central California feasible. Modelled and measured *TS* were comparable to available estimates, and the jelly-classification algorithm was effective at extracting sound-scatter attributed to jellies. Future studies should have increased confidence with the acquisition of a new midwater-trawl net and tows targeted to layers appearing more prominently at 38 kHz than at higher frequencies. Archived acoustic-transect data of Monterey Bay from 2001 through 2007 can now be analyzed for the distributions and abundances of scyphozoan jellies. The combination of time-series of distributions and abundances of jellies and leatherback turtles from acoustic and aerial surveys, respectively, may provide a comprehensive characterization of the central California foraging area of leatherback turtles.

LITERATURE CITED

Alvarez Colombo, G., Mianzan, H., and Madirolas, A. 2003. Acoustic characterization of gelatinous-plankton aggregations; four case studies from the Argentine continental shelf. ICES Journal of Marine Science, 60:650-657.

Alvarez Colombo, G., Benovic, A., Malej. A., Lucic, D., Makovec ,T., Onofri ,V., and Acha, M. 2009. Acoustic survey of a jellyfish-dominated ecosystem (Mljet Island, Croatia). Hydrobiologia, 616:99-111.

Benson, S.R., Forney, K.A., Harvey, J.T., Carretta, J.V., and Dutton, P.H. 2007. Abundance, distribution, and habitat of leatherback turtles (*Dermochelys coriacea*) off California, 1990-2003. Fishery Bulletin, 105:337-347.

Brierley, A.S., Axelsen, B.E., Beucher, E., Sparks, C.A.J., Boyer, H., and Gibbons, M.J. 2001. Acoustic observations of jellyfish in the Namibian Benguela. Marine Ecology Progress Series, 210:55-66.

Brierley, A.S., Axelsen, B.E., Boyer, D.C., Lynam, C.P., Didcock, C.A., Boyer, H., Sparks, C.A.J., Purcell, J.E., and Gibbons, M.J. 2004. Single target echo detections of jellyfish. ICES Journal of Marine Science, 61:383-393.

Brierley, A.S., Boyer, D.C., Axelsen, B.E., Lynam, C.P., Sparks, C.A., Boyer, H.J., and Gibbons, M.J. 2005. Towards the acoustic estimation of jellyfish abundance. Marine Ecology Progress Series, 295:105-111.

Chu, D., Foote, K.G., and Stanton, T.K. 1993. Further analysis of target strength measurements of Antarctic krill at 38 and 120 kHz: Comparison with a deformed cylinder model and inference of orientation distribution. Journal of the Acoustical Society of America, 93:2985-2988.

Demer, D.A., and Conti, S.G. 2003a. Reconciling theoretical versus empirical target strengths of krill: effects of phase variability on the distorted-wave Born approximation. ICES Journal of Marine Science, 60:429-434.

Demer, D.A., and Conti, S.G. 2003b. Validation of the stochastic distorted-wave Born approximation model with broad bandwidth total target strength measurements of Antarctic krill. ICES Journal of Marine Science, 60:625-635.

Demer, D., Soule, M.A., and Hewitt, R.P. 1999. A multiple-frequency method for potentially improving the accuracy and precision of *in situ* target strength measurements. Journal of the Acoustical Society of America, 105:2359 2376.

Dutton, P.H., Bowen, B.W., Owens, D.W., Barragan, A., and Davis, S.K. 1999. Global phylogeography of the leatherback turtle (*Dermochelys coriacea*). Journal of Zoology, London 248:397-409.

Fleischman, S., and Burwen, D. 2000. Correcting for position-related bias in estimates of the acoustic backscattering cross-section. Aquatic Living Resources, 13:283-290.

Francois, R., and Garrison, G. 1982. Sound absorption based on ocean measurements- 2. Boric acid contribution and equation for total absorption. Journal of the Acoustical Society of America, 72: 1879-1890.

Graham, W.M., Field, J.G., and Potts, D.C. 1992. Persistent "upwelling shadows" and their influence on zooplankton distributions. Marine Biology, 114:561-570.

Graham, W.M., and Largier, J.L. 1997. Upwelling shadows as nearshore retention sites: the example of northern Monterey Bay. Continental Shelf Research, 17:509-532.

Graham, W.M., Pages, F., and Hamner, W.M. 2001. A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia, 451:199-212.

Greenlaw, C.F., and Johnson, R.K. 1983. Multiple-frequency acoustical estimation. Biological Oceanography, 2:227-252.

Houghton, J.D.R., Doyle, T.K., Davenport, J., and Hays, G.C. 2006. Developing a simple, rapid method for identifying and monitoring jellyfish aggregations from the air. Marine Ecology Progress Series, 314:159-170.

Ishii, H., and Båmstedt, U. 1998. Food regulation of growth and maturation in a natural population of *Aurelia aurita* (L.). Journal of Plankton Research, 20:805-816.

Johannesson, K.A., and Mitson, R.B. 1983. Fisheries acoustics: a practical manual for aquatic biomass estimation. FAO Fisheries Technical Paper, 240:249.

Lucas, C.H. 2001. Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. Hydrobiologia, 451:229-246.

Lucas, C.H., and Lawes, S. 1998. Sexual reproduction of the scyphomedusae *Aurelia aurita* in relation to temperature and variable food supply. Marine Biology, 131:629-638.

Monger, B.C., Chinniah-Chandy, S., Meir, E., Billings, S., Greene, C.H., and Wiebe, P.H. (1998) Sound scattering by the gelatinous zooplankters *Aequorea victoria* and *Pleurobrachia bachei*. Deep-Sea Research Part II, 45:1255-1271.

Mutlu, E 1996. Target strength of the common jellyfish (*Aurelia aurita*): a preliminary experimental study with a dual-beam acoustic system. ICES Journal of Marine Science, 53:309-311.

Stanton, T.K., Wiebe, P.H., Chu, D., Benfield, M., Scanlon, L., Martin, L., and Eastwood, R.L. 1994. On acoustic estimates of zooplankton biomass. ICES Journal of Marine Science, 51:505-512.

Stanton, T.K., Chu, D., and Wiebe, P.H. 1996. Acoustic scattering characteristics of several zooplankton groups. ICES Journal of Marine Science, 53:289-295.

Stanton, T.K., Chu, D., Wiebe, P.H., Martin, L.V., and Eastwood, R.L. 1998. Sound scattering by several zooplankton groups. Experimental determination of dominant scattering mechanisms. Journal of the Acoustical Society of America, 103:225-235.

Warren, J.D., and Smith J.N. 2007 Density and sound speed of two gelatinous zooplankton: Ctenophore (*Mnemiopsis leidyi*) and lion's mane jellyfish (*Cyanea capillata*). Journal of the Acoustical Society of America, 122:574-580.