1   Feeding ecology of broadbill swordfish (*Xiphias gladius*) in the California Current

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Abstract

25   The feeding ecology of broadbill swordfish (*Xiphias gladius*) in the California Current was

26   described based on analysis of stomach contents collected by federal fishery observers aboard

27   commercial drift gillnet boats from 2007 to 2014. Prey were identified to the lowest taxonomic level

28   and diet composition was analyzed using univariate and multivariate methods. Of 299 swordfish

29   sampled (74 to 245 cm eye-to-fork length), 292 non-empty stomachs contained remains from 60 prey

30   taxa. Diet consisted mainly of cephalopods but also included epipelagic and mesopelagic teleosts.

31   Jumbo squid (*Dosidicus gigas*) and *Gonatopsis borealis* were the most important prey based on the

32   geometric index of importance. Swordfish diet varied with body size, location and year. Jumbo squid,

33   *Gonatus* spp. and Pacific hake (*Merluccius productus*) were more important for larger swordfish,

34   reflecting the ability of larger specimens to catch large prey. Jumbo squid, *Gonatus* spp. and market

35   squid (*Doryteuthis opalescens*) were more important in swordfish diet in inshore waters, while *G.*

36   *borealis* and Pacific hake predominated offshore. Jumbo squid was more important from 2007-2010

37   than in 2011-2014, with Pacific hake the most important prey item in the latter period. Diet variation

38   by area and year probably reflects differences in swordfish preference, prey availability, prey

39   distribution, and prey abundance. The range expansion of jumbo squid that occurred during the first

40   decade of this century may particularly explain their prominence in swordfish diet from 2007-2010.

41   Some factors that may influence dietary variation in swordfish were identified. Standardization could

42   make future studies more comparable for conservation monitoring purposes.

43

Introduction

45   Broadbill swordfish (*Xiphias gladius*, hereafter swordfish) are the most widely distributed

46   billfish and occur worldwide in tropical, subtropical and temperate waters from around 50°N to 50°S

47   [1-3]. They co-occur in the California Current Large Marine Ecosystem (CCLME), with several other

48   upper trophic-level predators such as sharks and dolphins [4, 5]. Swordfish are productive predators,

49   filling a similar ecosystem role to other large pelagic marine species, including other billfish species,

50   sharks, tunas and dolphins [6]. Swordfish command a high economic value in both commercial and

51   recreational fisheries in all oceans of the world [4]. In the CCLME, swordfish are landed in both the

52   U.S.A. and Mexico. In the U.S.A., they are the primary target of the drift gillnet (DGN) fishery that

53   operates mainly in the U.S. waters of the Southern California Bight (SCB). Swordfish are also landed

54   in the historic harpoon fishery, and more recently in the deep-set buoy gear fishery that was developed

55   as a low-bycatch method to target swordfish during daylight hours [7-9].

56   The swordfish population in the North Pacific is assessed as two stocks, divided by a boundary

57   extending from Baja California (25ºN x 110ºW) to 165ºW at the Equator [10, 11]. These are the

58   Western and Central North Pacific Ocean (WCNPO) stock and the Eastern Pacific Ocean (EPO) stock

59   [3, 12, 13]. The most recent stock assessment indicated that the WCNPO stock, which is the source of

60   the DGN fleet swordfish catch, was neither overfished nor experiencing overfishing [13].

61   Swordfish are well adapted for survival in a wide range of water temperatures from 5°C to

62   27°C; however, they are generally found in areas with sea surface temperatures (SST) above 13°C

63   [14]. They are highly fecund and do not seem to have discrete spawning grounds or seasons [15].

64   Swordfish migration patterns have not been described in peer-reviewed publications, although tag

65   release and recapture data indicate an eastward movement from the central Pacific, north of Hawaii,

66   towards the U.S. West Coast [4]. Swordfish tend to concentrate near underwater features, like

67   seamounts and banks, and near oceanographic boundaries where sharp gradients of temperature and

68   salinity exist [1], such as convergence zones and strong thermoclines [16]. These regions are known

69   for having a relatively high abundance of forage species [17, 18]. Swordfish aggregate along these

70   productive thermal boundaries between cold upwelled water and warmer water masses to forage [16,

71   19] and do not travel far during the first year of life [20].

72   Further insights into foraging come from information on vertical movement patterns.

73   Swordfish display diurnal vertical migration, diving below the deep scattering layer by day and

74   returning to shallower depths by night. Daytime depth distribution is hence more variable, including

75   periods of basking behavior when swordfish are visibly present at the ocean surface, compared to a

76   narrow depth range at night when it is concentrated near the surface [21-23]. During dives, swordfish

77   can reach depths of up to 1000 m, indicating a tolerance of low water temperatures (c. 5°C).

78   Like other billfish, swordfish have a number of adaptations that enhance foraging ability. They

79   use their large bill to incapacitate and kill prey [1, 24]. Though they swim relatively fast, their large

80   size limits maneuverability [25]. Partial endothermy and large eyes enhance foraging at depth [26].

81   Swordfish have also evolved a specialized muscle that functions as a brain heater. This

82   mechanism allows them to function in cold water, which is essential to a fast-swimming predator that

83   generally hunts on the cooler side of boundaries between oceanic water masses [1, 26-28].

84   Endothermy also has energy costs, suggesting that swordfish may have higher energy needs than

85   otherwise similar heterothermic species [24]. Thus, they need to catch more energy-rich prey or

86   consume a greater quantity of prey than would be necessary if they were ectothermic.

87   Although they can use their sword to subdue prey items for easier consumption [29],

88   swordfish lack teeth and ingest their food whole, physically limiting the size of prey they can handle.

89   By contrast, sharks use their sharp teeth to tear and consume very large prey piecemeal. The

90   combination of large size, endothermy, and the lack of slicing teeth possibly places swordfish closer

91   to dolphins rather than sharks in terms of foraging ecology. Swordfish diets and prey composition

92   have been found to vary by ecosystem. In some regions, swordfish diets presented a prevalence of

93   teleosts, while in others cephalopods were most prominent. In a few areas, a similar proportion of

94   both prey item groups were observed (Table 1). Several studies considered only the cephalopod

95   portion of the swordfish diet and, therefore, are not listed in Table 1 [30-34].

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99 **Table 1.** Proportion of teleosts and cephalopods, by area, in diet of swordfish based on published

100 studies. '*' = highest proportion; W=Western; N=North E=Eastern; S=Southern; Teleo=teleosts;

101 Ceph=cephalopods.

Area	Teleo	Ceph	Authors
W. N. Atlantic	*		[29], [35-48]
		*	[49, 50]
E. N. Atlantic	*	*	[51-53]
		*	[54, 55]
E. Central Atlantic	*	*	[56, 57]
E. Tropical Atlantic		*	[58]
Tropical Atlantic	*		[59]
W. Equatorial Indian Ocean	*		[60]
E. N. Pacific (Channel Islands, California)	*		[61]
E. N. Pacific (Baja California)	*	*	[62]
		*	[63]
Central N. Pacific (Hawaii)		*	[64]
E. Pacific (Chile)		*	[65-69]
	*		[70]
E. Pacific (Ecuador)		*	[71, 72]
S. Pacific	*		[73]
W. N. Pacific		*	[74]
E. Mediterranean Sea		*	[75]
S. Aegean Sea	*		[76]
E. Australia		*	[77]

102

103 Southern California is a foraging ground within the CCLME where swordfish from various

104 regions of the eastern and central north Pacific aggregate. While the CCLME is known to be an

105 important foraging ground for swordfish during certain times of year, the feeding habits of swordfish

106   in this region are not well documented, especially in recent years. To date, there have been two

107   extensive studies of swordfish feedings habits in the CCLME [62, 63] as well as a few other less

108   comprehensive studies [61, 78, 79]. This study aims to expand our knowledge of the feeding ecology

109   of swordfish in the CCLME by analyzing the: (1) relative importance of different prey types; and (2)

110   dietary variation inter-annually, by sub-period (within years), by area, and in relation to body size.

111   The findings of this study can serve to inform the development of alternative approaches to better

112   manage this economically and ecologically important species.

113

Methods

Sampling at sea

Federal fishery observers aboard DGN vessels collected swordfish stomachs during the 2007-2014 fishing seasons. The DGN vessels operate within the U.S. EEZ, primarily in the SCB from August 15 through January 31. Because the season spans two calendar years, 'year' for this study refers to the fishing season, e.g., 2007 refers to August 2007 through January 2008. Sets are conducted using 1.8 km long drift gillnets extending from roughly 12 m to 100 m below the surface. DGN boats are active at night, setting nets within one hour before sunset and hauling in within one hour after sunrise for an average net-soaking time of approximately 12 hours. Hauling can then take 4 to 6 hours.

Stomach samples were excised at sea, the oesophageal and pyloric ends secured with plastic cinch ties, and the stomachs then bagged, labeled and frozen. Additional data recorded at sea included set and haul-back times, water depth, SST, date, location and fish size.

Processing in the laboratory

Stomachs were thawed, tamped with absorbent paper to remove excess water, and weighed full. Contents were then removed and the empty stomach lining weighed to obtain overall contents weight. Solid material and slurry were rinsed and sorted using a series of mesh screen sieves with mesh sizes 9.5 mm, 1.4 mm, and 0.5 mm for ease of rinsing mid-sized food boluses without losing some of the smallest items, such as fish otoliths. Degree of prey digestion was estimated using a six-point scale as follows: (1) Fresh: head, body, skin and most fins intact though some individuals may be in pieces (i.e., sliced on capture); (2) Intermediate: body and most flesh intact; fins, scales and

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136   some or all cephalopod skin may be digested; (3) Intact skeleton from head to hypural plate or

137   body/mantle/carapace intact, or easily reconstructed to obtain standard length measurements; (4)

138   Unmeasurable body parts only: hard parts cannot be reassembled to obtain standard measurements,

139   but higher taxon or species group still identifiable; (5) Digested but identifiable to a higher taxonomic

140   level (e.g., family); and (6) Fully digested unidentifiable material; slurry. Prey items were then

141   separated, identified to the lowest possible taxonomic level using taxonomic keys, enumerated,

142   measured and weighed. Fish otoliths and the upper and lower squid beaks were counted in pairs when

143   possible, with the highest count representing the minimum number present. These numbers were

144   added to the numbers of intact prey. Weights were grouped by taxon (not individually), while lengths

145   of all intact individuals within a taxon were measured. Weight of a taxon was the weight of the

146   undigested and partially digested items found in the stomach and not based on back-calculations of

147   weight at the time of ingestion from measurements of hard parts. This approach was chosen because

148   substantial amounts of undigested food remains were found and it is commonly used in studies of fish

149   stomach contents [80]. A consequence of this approach is that prey eaten longer ago contribute less to

150   the weight.

151   Partial remains comprising only large chunks (i.e., fist size or greater) or pieces of fish in

152   digestive state 1 or 2 were considered to be the result of swordfish feeding on prey caught in the

153   driftnet and therefore were discarded from the analysis.

154   Genetic analyses were used to identify diet items that could not be identified visually. Tissue

155   samples for DNA extraction were taken from the interior of the sample to minimize cross

156   contamination with other prey. DNA was extracted using a DNeasy blood and tissue kit (Qiagen)

157   following the manufacture's protocols. The "Barcode" region of the mitochondrial cyctochrome c

158   oxidase I (COI) gene was amplified by polymerase chain reaction (PCR) following [81], using their

159   COI-3 primer set with M13 tails. No template negative controls were run for each PCR batch to

160   monitor for potential DNA contamination of reagents. PCR products were sequenced using BigDye v

161   3.1 dye terminator chemistry (Life Technologies), using the sequencing primers M13F(-21) and

162   M13R(-27) following manufacturers' protocols. Aligned and edited sequences were entered into the

163   BOLD v4 [82] and matches greater than 98% identity to a single taxon were considered to be the

164   correct species assignment for the prey item.

165   Secondary prey items (prey of prey) were discarded when found associated with the stomachs

166   of fresh prey (e.g., euphausiids in the stomachs of Pacific hake). In other cases, the presence of

167   secondary prey cannot be ruled out. This is a common issue in diet analysis but is generally

168   considered to have only minor consequences for the estimated biomass of different prey categories

169   [62, 83].

170

Data analysis

172   Randomized cumulative curves depicting the relationship between number of prey taxa

173   detected and sample size (rarefaction curves) were constructed using the Vegan package [84] in R

174   statistical software [85] to determine the extent to which the sample size characterize the diet [86-90].

175   For this analysis, the order in which stomach contents were analyzed was randomized 100 times and

176   the mean (± 2 standard deviations) number of prey taxa observed was plotted against the number of

177   stomachs examined. A curve approaching an asymptote with low variability indicates that the number

178   of stomachs examined is sufficient to characterize the diet [86]. To complement this visual approach,

179   a method proposed by [91] was used to assess whether the curve had reached an asymptote.

180   Specifically, a straight line was fitted to the rightmost 4 points of the species accumulation curve. If

181   the slope did not differ significantly from zero, then the species accumulation curve was inferred to

182   have reached an asymptote. For constructing such cumulative prey curves, [91] lumped prey into

183   higher-level taxonomic categories (e.g., crustaceans, teleosts, polychaetes). By contrast, we used the

184   lowest taxonomic level to which prey had been identified, making it much less likely that the curves

185   would reach an asymptote and assuring that the curves gave a more reliable picture of the adequacy of

186   sample size to fully describe diet. Prey identified to species as well as unidentified categories were all

187   included in the analysis. In general, if the proportion of unidentified prey species in the diet is low, the

188   rarefaction curve tends to be a good guide to how many samples are required to sufficiently

189   characterize diet. If the proportion of unidentified species is high, confidence in the curve will be

190   lower, but it can remain a helpful tool.

191   The importance of each prey type was summarized using three standard Relative Measures of

192   Prey Quantities (RMPQs): percent frequency of occurrence (%F); percent composition by number

193   (%N); and percent composition by weight (%W) [80, 83, 92, 93]. Stomachs which were empty or

194   contained only slurry and/or detritus were not considered when calculating percentages. Two

195   combined dietary indices (in both cases expressed both in original form and as percentages) were also

196   used to rank prey taxon importance, namely the geometric index of importance (GII) and percentage

197   GII (%GII) [94], and the index of relative importance (IRI) and percentage IRI (%IRI) [92]. These are

198   useful indices to rank prey importance since they take into account both numerical and weight-based

199   importance to the diet. Some authors favor GII [95-97] and others favor IRI [98-100], while some

200   doubt the merits of all such combined indices (see [83] and references therein). Here, each method

201   was used to examine only the ranking of prey types, because the two combined index values are not

202   directly comparable.

203   The GII, in its simplified form, is calculated as:

204

$$GII_j = \frac{\left(\sum\limits_{i=1}^{n} V_i\right)_j}{\sqrt{n}}$$

205   where GII_j = index value for the j-th prey category, V_i = the magnitude of the vector for the i-th

206   RMPQ of the j-th prey category, and n = the number of RMPQs used in the analysis (in this case 3,

207   since we used %W, %N and %F).

208   The %GII_j converts GII_j values to a percentage scale:

209

$$\%GII_j = \frac{\left(\sum\limits_{i=1}^{n} V_i\right)_j}{n}$$

210   The IRI for the j-th prey category is calculated as:

211
$$IRI_j = (\%N_j + \%W_j) * \%F_j$$

212   The IRI value was also converted to a percentage, which is arguably more useful for comparisons

213   among studies [101]:

214
$$\%IRI_j = 100\ IRI_j / \sum\limits_{j=1}^{n} IRI_j$$

215   To analyze overall variation in swordfish diet in relation to body size, fishing area (within the

216   SCB and beyond the SCB areas) and year, samples were categorized into groups: (1) 'Small' (< 165

217   cm) and 'Large' ($\geq$ 165 cm) size categories, based on eye-to-fork length (EFL), with the cut-off

218   chosen to produce similar samples sizes for each group; (2) 'Within SCB' (east of 120º 30'W) and

219   'Beyond SCB' (west of 120º 30'W) (this longitude approximately separates the waters in the SCB

220   where the northward flowing California Counter Current influences nearshore oceanography and the

221   more offshore waters affected by the California Current as it moves southward); and (3) 'Year' was

11

222   assigned based on the DGN fishing season, August 15 through January 31, such that all specimens

223   collected in a single fishing season were assigned the year of the season's start date.

224   Differences in diet across size-, area- and year-groups were quantified and their statistical

225   significance estimated using bootstrap simulations. In each case of the six most important prey items

226   overall, 1000 bootstrap replicates of GII values for both groups were generated (e.g., GII for jumbo

227   squid in stomachs of (A) small and (B) large fish) and, for each replicate, it was noted whether GII

228   was higher in the first subgroup or in the second subgroup. If the GII value in A was higher than the

229   GII value in B in more than 95% of replicates, we argue that the species is significantly more

230   important in the diet of group A than in the diet of group B (and vice versa). All measures were

231   calculated using R statistical software [85]. No index value was estimated if the sample size was less

232   than 10, since small samples are known to produce biased values [102].

233   To summarize relationships between diet composition in terms of the importance of different

234   prey items (response variables) and potential explanatory factors, redundancy analysis (RDA) was used,

235   as implemented in Brodgar 2.7.4 (www.brodgar.com). Rare prey taxa that were found in less than 4

236   stomachs were removed prior to this analysis. The swordfish sample comprised 289 individuals (samples

237   with food and EFL available) and the effects of 7 explanatory variables were considered: area (east and

238   west of 120°30'W), time period (2007, 2008-2010, 2011-2014), half-year (August 15 through November

239   7 and November 8 through January 31), predator size (EFL) and SST (which was available for each haul

240   and was measured at the beginning of the set). Years were grouped to avoid an excessive number of

241   explanatory variables in relation to the sample size and to retain reasonable sample sizes per group.

242   Categorical variables were replaced by "dummy" variables. That is, a variable with X categories is

243   replaced by X-1 binary (0-1) variables, each signifying that the original categorical variable takes or does

244   not take a particular value. In all analyses, only X-1 binary variables are entered because once the value

12

245   of all these is specified the value of the last one is already known. Data were transformed using Chord

246   distance [103-105], a method that allows assignment of a low weighting to rare prey species.

247   To examine the relationship between the importance of individual prey types and the various

248   explanatory variables, Generalized Additive Modelling (GAM) was used. GAM is an extension of the

249   regression-based statistical modelling approach that is suitable when the response variable is not

250   (necessarily) normally distributed and there is no reason to expect linear relationships between response

251   and explanatory variables. In linear regression, the slope values (regression coefficients) quantify the

252   relationships between the response variable and each of the explanatory variables, while GAM uses

253   "smoothing" functions to capture these relationships. The default smoothing function used in the GAM

254   function in the *mgcv* package in R [106] (and also used in Brodgar statistical software) is the thin plate

255   regression spline. The complexity of the resulting curve is normally determined by the fitting routine

256   ("cross-validation") but can be restricted by the user, and is summarized in the "degrees of freedom",

257   with high values indicating more complex curves. If the degrees of freedom of a smoother are equal to or

258   close to 1, this implies an approximately linear function. When applying GAM, it is necessary to

259   consider the distribution of the response variable, which is likely to depend on the nature of the variable

260   studied. In this study, the data are in the form of prey counts for the main prey species. Some prey

261   occurred in large numbers and the distribution of the number of prey per stomach is likely to be strongly

262   right-skewed, hence a negative binomial distribution was used. The number of knots, k, was limited to 4

263   to avoid overfitting in the case of explanatory variables for which relatively simple relationships would

264   be expected, e.g., body size. The forwards selection method was used for model fitting. To avoid the

265   model misspecification, the optimal GAM model was validated by checking for influential data points

266   and looking for patterns in the distribution of residuals [107, 108]. GAMs were fitted using count data

267   for all of the top seven ranked prey items (based on GII).

Results

Sample composition

A total of 299 broadbill swordfish (*Xiphias gladius*) stomachs were collected during 103 observed DGN trips in the CCLME (Fig 1). Samples were collected from 2007-2014 throughout the CCLME but especially in the southeast, where the fishing is mainly concentrated. SST at the time of sample collection ranged from 14.3°C to 21.9°C (mean 17.9°C). Swordfish ranged in size from 74 to 245 cm EFL (Fig 2). [109] provided median body size at sexual maturity (L50) for males (102 cm ± 2.5 (95 % CI) cm EFL) and females (144 ± 2.8 cm EFL). Based on these estimates, almost all the animals in this study were above the typical size at maturity for males and a majority were above the typical size at maturity for females; as noted above, sex was not determined. Of the 299 swordfish stomachs examined, 292 contained food remains belonging to 60 different prey taxa overall. Ninety-one percent of the food items were in an advanced state of digestion (stages 4 and 5).

Fig 1. Collection areas of swordfish used for diet analysis. Number of samples is indicated by greyscale in the legend. Map shows the northern part of the CCLME that extends to the tip of Baja California.

Fig 2. Length-frequency distribution of swordfish sampled in the diet study. *N*=295. *Arrows* indicate typical sizes at maturity for males and females [109]. Eye-to-fork length is measured in cm. (Size was not determined for 4 individuals of the 299 sampled).

Sample size sufficiency

291

292   The cumulative prey curve did not reach an asymptote for the swordfish stomachs analyzed

293   (Fig 3). The terminal portion of the curve (4 last points) had a slope that differed significantly from

294   zero (p = 0.0009). Nevertheless, the fact that the curve starts to asymptote indicates that the majority

295   of prey taxa present in the diet of the swordfish (at the temporal and spatial scale of the present study)

296   are likely to be represented in these analyses.

297

298   **Fig 3.** Cumulative prey curve (rarefaction curve) for swordfish (prey identified at the lowest possible

299   taxonomic level).

300

Indices of prey importance

301

302   Table 2 lists each of the RMPQs for all prey found, as well as the calculated GII, %GII, IRI

303   and %IRI values. Rankings of prey taxa based on GII and IRI were nearly identical. Jumbo squid

304   (*Dosidicus gigas*) was the most important prey item by weight, number and according to the two

305   combined indices. The boreopacific gonate squid (*Gonatopsis borealis*) was the second most

306   important prey according to GII and IRI, and the most important by frequency of occurrence. Other

307   important squid prey included *Abraliopsis* sp., *Gonatus* spp. and market squid (*Doryteuthis*

308   *opalescens*). Pacific hake (*Merluccius productus*) was the highest ranked teleost prey species, ranked

309   sixth by GII. Swordfish also preyed on barracudinas (Paralepididae), several species of coastal pelagic

310   fishes (jack mackerel *Trachurus symmetricus*, Pacific sardine *Sardinops sagax*, Pacific saury

311   *Cololabis saira*, northern anchovy *Engraulis mordax*), luvar (*Luvarus imperialis*), king-of-the-salmon

312   (*Trachipterus altivelis*), halfmoon (*Medialuna californiensis*) and seven species of the family

15

313   Myctophidae (Table 2). Cuts and punctures were apparent on several of prey items.

314

315   **Table 2.** Quantitative prey composition of the broadbill swordfish (*Xiphias gladius*) in the CCLME.

316   A total of 299 stomachs (292 containing food and 7 without food) was examined. Prey items are

317   shown in order of decreasing GII value. W = weight (g) for the given prey taxon, %W is the same

318   value expressed as a percentage of the total weight summed across all prey taxa, N = number of prey

319   individuals, F = frequency of occurrence (number of stomachs in which the prey taxon occurred), %F

320   = frequency of occurrence expressed as a percentage of the number of (non-empty) stomachs

321   examined; GII = geometric index of importance (%W+%N+%F)/$\sqrt{3}$; IRI = index of relative

322   importance (%W+%N)*%F.

323

Prey Taxon	W (g)	%W	N	%N	F	%F	GII	%GII	IRI	%IRI
Jumbo squid, *Dosidicus gigas*	131892.7	53.27	1061	20.23	173	59.25	76.64	44.25	4354.96	56.47
Boreopacific gonate squid, *Gonatopsis borealis*	19949.8	8.06	884	16.86	182	62.33	50.37	29.08	1552.94	20.14
Abraliopsis sp.	45.1	0.02	464	8.85	117	40.07	28.25	16.31	355.26	4.61
Gonatus spp.	181.6	0.07	299	5.70	110	37.67	25.08	14.48	217.56	2.82
Market squid, *Doryteuthis opalescens*	1447.6	0.58	538	10.26	88	30.14	23.66	13.66	326.81	4.24
Pacific hake, *Merluccius productus*	36360.1	14.69	331	6.31	49	16.78	21.81	12.59	352.37	4.57
Duckbill barracudina, *Magnisudis atlantica*	4568.6	1.85	218	4.16	84	28.77	20.07	11.59	172.67	2.24
Unidentified Teleostei	2316.9	0.94	119	2.27	65	22.26	14.70	8.49	71.35	0.93
Chubby pearleye, *Rosenblattichthys volucris*	810.6	0.33	166	3.17	49	16.78	11.71	6.76	58.61	0.76
Jack mackerel, *Trachurus symmetricus*	6668.2	2.69	72	1.37	28	9.59	7.88	4.55	38.99	0.51
Nansenia spp.	510.9	0.21	124	2.36	32	10.96	7.81	4.51	28.17	0.37
Onychoteuthis borealijaponica	656.6	0.27	60	1.14	35	11.99	7.73	4.47	16.89	0.22
Slender barracudina, *Lestidiops ringens*	330.0	0.13	92	1.75	29	9.93	6.82	3.94	18.75	0.24
Pacific pomfret, *Brama japonica*	5241.6	2.12	41	0.78	24	8.22	6.42	3.71	23.83	0.31
Pacific sardine, *Sardinops sagax*	1823.1	0.74	77	1.47	26	8.90	6.41	3.70	19.63	0.25
Luvar, *Luvarus imperialis*	19258.5	7.78	18	0.34	7	2.40	6.07	3.51	19.47	0.25
Pacific saury, *Cololabis saira*	1366.8	0.55	76	1.45	21	7.19	5.31	3.06	14.39	0.19
Unidentified Scopelarchidae	476.9	0.19	86	1.64	20	6.85	5.01	2.89	12.55	0.16
Cock-eyed squid, *Histioteuthis heteropsis*	1312.2	0.53	52	0.99	18	6.16	4.44	2.56	9.38	0.12

16

Feeding ecology of broadbill swordfish

Prey										
Pacific mackerel, *Scomber japonicus*	2180.7	0.88	66	1.26	16	5.48	4.40	2.54	11.72	0.15
Sunbeam lampfish, *Lampadena urophaos*	201.9	0.08	42	0.80	18	6.16	4.07	2.35	5.44	0.07
King-of-the-salmon, *Trachipterus altivelis*	5577.4	2.25	25	0.48	13	4.45	3.86	2.39	10.59	0.16
Flowervase jewell squid, *Histioteuthis dofleini*	560.1	0.23	25	0.48	15	5.14	3.37	1.95	3.61	0.05
Unidentified Eucarida	5.5	<0.01	154	2.94	6	2.05	2.88	1.67	6.04	0.08
Unidentified Teuthoidea	202.0	0.08	15	0.29	12	4.11	2.58	1.49	1.51	0.02
Spotted barracudina, *Arctozenus risso*	67.9	0.03	14	0.27	8	2.74	1.75	1.01	0.81	0.01
Histioteuthis spp.	56.7	0.02	9	0.17	8	2.74	1.69	0.98	0.53	0.01
Argonauta sp.	13.1	0.01	8	0.15	8	2.74	1.67	0.97	0.43	0.01
Striped mullet, *Mugil cephalus*	1737.8	0.70	8	0.15	4	1.37	1.28	0.74	1.17	0.02
Octopoteuthis sp.	2.1	<0.01	6	0.11	6	2.05	1.25	0.72	0.24	<0.01
Bigfin lampfish, *Symbolophorus californiensis*	5.4	<0.01	7	0.13	5	1.71	1.07	0.62	0.23	<0.01
Sharpchin barracudina, *Stemonosudis macrura*	8.8	<0.01	8	0.15	4	1.37	0.88	0.51	0.21	<0.01
Cranchia scabra	4.5	<0.01	5	0.10	4	1.37	0.85	0.49	0.13	<0.01
Mexican lampfish, *Triphoturus mexicanus*	<0.1	<0.01	4	0.08	4	1.37	0.83	0.49	0.10	<0.01
Paralepididae, Barracudinas	111.3	0.04	7	0.13	3	2.40	1.49	0.86	0.43	0.01
Unidentified Euphausiidae	3.0	<0.01	6	0.11	3	2.05	1.25	0.72	0.24	<0.01
Robust clubhook squid, *Onykia robusta*	43.3	0.02	4	0.08	3	1.37	0.85	0.49	0.13	<0.01
Northern anchovy, *Engraulis mordax*	1.6	<0.01	4	0.08	3	1.37	0.84	0.49	0.11	<0.01
California smoothtongue, *Leuroglossus stilbius*	<0.1	<0.01	4	0.08	3	1.37	0.83	0.49	0.10	<0.01
Unidentified Tunicata	3.5	<0.01	3	0.06	3	1.03	0.63	0.37	0.06	<0.01
Smalleye squaretail, *Tetragonurus cuvieri*	161.9	0.07	3	0.06	2	1.03	0.66	0.39	0.13	<0.01
Onychoteuthis sp.	<0.1	<0.01	4	0.08	2	1.37	0.83	0.49	0.10	<0.01
Japetella sp.	<0.1	<0.01	4	0.08	2	1.37	0.83	0.49	0.10	<0.01
Splitnose rockfish, *Sebastes diploproa*	924.2	0.37	2	0.04	1	0.68	0.63	0.36	0.28	<0.01
Northern lampfish, *Stenobrachius leucopsarus*	<0.1	<0.01	2	0.04	2	0.68	0.42	0.24	0.03	<0.01
Octopus rubescens	<0.1	<0.01	2	0.04	2	0.68	0.42	0.24	0.03	<0.01
Chiroteuthis calyx	<0.1	<0.01	2	0.04	2	0.68	0.42	0.24	0.03	<0.01
Albacore, *Thunnus alalunga*	371.6	0.15	1	0.02	1	0.34	0.30	0.17	0.06	<0.01
Sebastes spp.	3.0	<0.01	8	0.15	1	2.74	1.67	0.97	0.42	0.01
Halfmoon, *Medialuna californiensis*	81.0	0.03	1	0.02	1	0.34	0.23	0.13	0.02	<0.01
Dogtooth lampfish, *Ceratoscopelus townsendi*	1.5	<0.01	2	0.04	1	0.68	0.42	0.24	0.03	<0.01
Shortbelly rockfish, *Sebastes jordani*	0.4	<0.01	2	0.04	1	0.68	0.42	0.24	0.03	<0.01
Leachia dislocata	<0.1	<0.01	2	0.04	1	0.68	0.42	0.24	0.03	<0.01
Pacific bonito, *Sarda chiliensis*	25.8	0.01	1	0.02	1	0.34	0.21	0.12	0.01	<0.01
Auxis sp.	4.7	<0.01	1	0.02	1	0.34	0.21	0.12	0.01	<0.01
Mastigoteuthis dentata	<0.1	<0.01	1	0.02	1	0.34	0.21	0.12	0.01	<0.01
Octopus spp.	<0.1	<0.01	1	0.02	1	0.34	0.21	0.12	0.01	<0.01
California flashlightfish, *Protomyctophum crockeri*	<0.1	<0.01	1	0.02	1	0.34	0.21	0.12	0.01	<0.01

California headlightfish, *Diaphus theta*	<0.1	<0.01	1	0.02	1	0.34	0.21	0.12	0.01	<0.01
Unidentified Isopoda	<0.1	<0.01	1	0.02	1	0.34	0.21	0.12	0.01	<0.01

324

325

326   In general, both large and small swordfish fed on similar prey but some differences were

327   apparent. Based on GII results, jumbo squid was the most important prey item followed by the *G.*

328   *borealis*, and *Abraliopsis* sp., in both size classes. However, northern anchovy was found only in

329   stomachs of the small size group while luvar was eaten only by large swordfish (Table S1 and S2).

330   Jumbo squid, *Gonatus* spp., and Pacific hake were significantly more important in larger swordfish

331   than smaller swordfish (Table S3).

332   A comparison of the GII results by area indicated that jumbo squid and *G. borealis* were the

333   two most important prey of swordfish in both areas. The third ranked species were *Abraliopsis* sp.

334   within the SCB, and Pacific hake beyond the SCB. Striped mullet (*Mugil cephalus*), northern anchovy

335   and *Sebastes* spp. were recorded only within the SCB (Table S4 and S5). Jumbo squid, *Gonatus* spp.

336   and market squid were significantly more important within the SCB than beyond the SCB, while *G.*

337   *borealis* and Pacific hake were significantly more important beyond the SCB (Table S6).

338   Between-year comparisons showed that jumbo squid was the first ranked prey, followed by *G.*

339   *borealis*, in 2007, 2008, 2010, 2012 and 2013. The importance of jumbo squid, *G. borealis*, *Gonatus*

340   spp., market squid and Pacific hake in the diet all varied significantly between years over the study

341   period (Table S15). In 2009, *G. borealis* was the most important prey followed by jumbo squid. In

342   2011 and 2014, Pacific hake ranked first followed by *G. borealis*. Pacific hake was not present in the

343   samples from 2008 through 2010. *Abraliopsis* sp. was important overall (ranked third) but was not

344   present in 2012. *Gonatus* spp. ranked fourth overall but was not present in the diet in 2011 (Table S7-

345   S14).

Redundancy Analysis (RDA)

347   Explanatory variables related to fish length (EFL), area, year and half-year, all significantly

348   affected the overall pattern of variation in diet (numerical importance of prey) in swordfish (Table 3).

349   Diet was significantly different (versus other years) in 2007 and 2011-2014. The set of explanatory

350   variables used explained 6 % of the overall variation in prey counts, with RDA axes 1 and 2

351   accounting for 36.9 % and 23.1 % of this variation respectively. The first two RDA axes thus explain

352   around 3.8 % of variation in prey counts, i.e., although significant temporal, spatial and size-related

353   variation in diet has been demonstrated, the majority of observed dietary variation remains

354   unexplained.

355

356   **Table 3.** Results of redundancy analysis (RDA) of variation in diet composition of swordfish (based

357   on prey numbers). Values of F and associated probability (p-value) are tabulated for two sets of model

358   runs. The variable 'year' (fishing season) was divided into three categories (2007, 2008-2010 and

359   2011-2014) and converted into three (0,1) dummy variables. Since the category may be identified

360   once the values of two of the dummy variables have been defined, all three dummy variables cannot

361   be included in the same run of the model. Left: model runs excluding 2011-2014. Right: model runs

362   excluding 2007. (EFL = eye to fork length, Area = east and west of 120°30'W, Half-year = August

363   15th through November 7th and November 8th through January 31st).

Variable	F-statistics	p-value	F-statistics	p-value
EFL	4.117	**0.005**	4.254	**0.005**
Area	3.896	**0.005**	3.895	**0.005**
2007	3.383	**0.005**		
Half-year	2.025	**0.005**	2.123	**0.005**
2011-2014			5.016	**0.005**
2008-2010	3.568	**0.005**	1.042	0.415
SST	0.758	0.785	0.758	0.815

364

19

365 Generalized Additive Models (GAMs)

366   To investigate sources of variation in the importance of individual prey taxa, binomial GAMs

367 were fitted for presence/absence of each the seven most important prey taxa, as ranked by GII. For

368 jumbo squid, the final model contained significant effects of SST, EFL and year (Table 4). The

369 presence of jumbo squid in swordfish stomachs was highest with SST around 21.5°C, it showed a

370 linear increase with increasing swordfish length, and it was lowest in 2009 and highest in 2007 (Fig

371 4*a*). The final model for *G. borealis* contained effects of year and area (Table 4). The presence of *G.*

372 *borealis* in swordfish stomachs was highest in 2009 and lowest around 2012 (Fig 4*b*), and was higher

373 beyond the SCB area than within.

374

375 **Table 4.** Effect of explanatory variables on the presence of the main prey taxa in swordfish diet (form

376 and direction of the relationship and statistical significance). The first row for each species-variable

377 combination contains the estimated degrees of freedom (edf) in the case of smoothers. The second

378 row indicates the probability. Only significant effects, retained in the final models, are shown.

379 Swordfish body length was measured as eye-to-fork length (EFL, cm). DE = deviance explained, AIC

380 = value of the Akaike Information Criterion. Blank cells indicate non-significant effects that were

381 dropped during model selection. 1st = first half of year, 2nd = second half of year; IN=within the SCB,

382 OFF = beyond the SCB subregion.

383

Swordfish	EFL	Year	SST	Half-year	Area	DE	AIC
Jumbo squid	1.0 (+)	2.9 (∪)	2.5 (+)			25.0	1073.6
	P<0.0001	P<0.0001	P<0.0001				
Gonatopsis borealis		2.9 (∩)			OFF>IN	14.5	963.97
		P<0.0001			P=0.0105		
Abraliopsis sp.	1.0 (+)	2.9 (∩)				9.8	727.51
	P=0.0468	P=0.0031					
Gonatus spp.		2.8 (∪)		1st>2nd		13.4	632.83
		P=0.0058		P=0.0049			

Market squid		2.8 (∩) P<0.0001		IN>OFF P=0.0050	21.6	683.98
Pacific hake	2.7 (+) P=0.0183	2.0 (+) P=0.0004			26.6	355.48
Duckbill barracudina		2.9 (∩) P=0.0002	2nd>1st P=0.0097	OFF>IN P=0.0053	20.7	496.50

384

385 For *Abraliopsis* sp., the final model contained effects of year and length (Fig 4*c*). The presence

386 of *Abraliopsis* sp. in swordfish stomachs was lowest in 2014 and highest in 2012, and showed a linear

387 increase with increasing swordfish length (Fig 4*c*). For *Gonatus* spp. the final model contained effects

388 of year and half-year (Table 4). The presence of *Gonatus* spp. in swordfish stomachs was highest

389 around 2008-2009 and 2014 and was lowest in 2012 (Fig 4*d*). Numbers of *Gonatus* spp. were higher

390 in the first half-year (August 15 through November 7) than in the second (Table 4).

391 For market squid, the final model contained effects of year and area (Table 4). The presence of

392 market squid in swordfish stomachs was highest in 2010 (Fig 4*e*) and was higher within the SCB area

393 than beyond it. For Pacific hake, the final model contained effects of year and length (Table 4). The

394 presence of Pacific hake in swordfish stomachs was highest in 2012 and showed a positive

395 relationship with fish length at lengths between around 125 and 150 cm (Fig 4*f*). For duckbill

396 barracudina, the final model contained effects of year, area, and half-year (Table 4). The presence of

397 duckbill barracudina in swordfish stomachs was highest in 2009 (Fig 4*g*). It was greater beyond the

398 SCB area and during the second half of the fishing season (November 8 through January 31).

399

400 **Fig 4.** GAM smoothing curves fitted to partial effects of explanatory variables on the presence of 7

401 prey taxa in the stomach of swordfish. EFL = eye-to-fork length. Dashed lines represent 95%

402 confidence intervals around the main effects.

403

Discussion

Swordfish display several notable adaptations that might be expected to influence their selection of prey items among the range of species present in the CCLME. Swordfish have cranial endothermy [27], with brain temperature elevated by up to 10°C-15°C above the temperature of the surrounding water when swimming [25], resulting in superior vision. Warming the brain and eyes may allow swordfish to remain active and responsive, increasing their visual threshold throughout the wide range of temperatures encountered in their vertical and migratory movements, permitting exploitation of different environments and prey [25]. The use of the "sword" for immobilizing or killing prey has been reported in past studies [29, 41, 46, 50] and a number of prey items in this study showed signs of being slashed, punctured or cut. The "sword" has a similar hunting function as the thresher's tail [110] and can be used to stun fish [111]. Adult swordfish are toothless [112] and swallow their prey whole. Interactions between whales and billfish have been occasionally observed [113] and records of fractured swords embedded in whales can be found in the literature [114-118] but there is no evidence of billfish feeding attacks on whales.

Vertical movements allow pelagic predators to extend their prey base or access different resources. In marine ecosystems, diel changes in distribution or behavior of predators are frequently in tune with diel changes in prey distribution, such as vertical migration of organisms associated with the deep scattering layer (DSL) [119]. The diurnal vertical distribution of swordfish is region-specific and likely influenced by both abiotic (temperature, thermocline depth, dissolved oxygen) and biotic factors (prey abundance and distribution, body temperature) [21]. Swordfish can feed at great depths during diurnal vertical migrations [26] and can feed during both day and night within the DSL [120]. Electronic tagging studies on swordfish in the CCLME show that these predators are capable of

426   exhibiting highly variable movements during the day but are consistently found within the upper

427   mixed layer at night [21, 23]. These movements are consistent with those of the DSL.

428   Results of the present study indicate that swordfish fed mainly on cephalopods and teleosts,

429   the most important prey taxa being jumbo squid (*Dosidicus gigas*), *Gonatopsis borealis* and

430   *Abraliopsis* sp., while teleosts included both epipelagic and mesopelagic species. Results are thus in

431   broad agreement with those from several studies of this species in other regions [34, 50, 55, 62, 63,

432   75, 77], although the relative importance of fish and cephalopods varies between different areas (see

433   Table 1).

434   Jumbo squid was an important prey item for swordfish in the CCLME, as was also the case for

435   several shark species (for mako, blue and bigeye thresher) in the area [5]. This finding is likely linked

436   to the range expansion of jumbo squid that started around 2002 in the CCLME. These cephalopods,

437   rarely found in the CCLME previously, greatly extended their range in the eastern North Pacific

438   Ocean during a period characterized by ocean-scale warming, regional cooling, and the decline of

439   tuna and billfish populations throughout the Pacific [121, 122]. Jumbo squid belong to the

440   Ommastrephidae, a family of largely pelagic squids that includes several species that support

441   important commercial squid fisheries around the world [123]. Ommastrephids, in general, have been

442   described as the most important cephalopod prey for swordfish in other regions of the world [29, 46,

443   47, 49, 50, 52, 54, 56, 58, 62, 64, 75] in both coastal and pelagic ecosystems.

444   Of the squids eaten by swordfish, while ommastrephids, gonatids and onychoteuthids, are

445   mainly epipelagic and all are powerful swimmers, the histioteuthids are predominantly mesopelagic

446   drifters [63], indicating that swordfish can feed in different environments. Since swordfish detect their

447   prey visually [26], swordfish may more easily catch fast-swimming, medium to large cephalopods

448   than small, slow-moving prey [63].

449   Pacific hake was, overall, the most important teleost species in the diet, based on ranking by

450 GII, followed by duckbill barracudina. Scombrids were also present in the diet. Merlucciids,

451 paralepidids, and scombrids have been described as important fish prey species of swordfish in a

452 number of other studies in different areas [29, 46, 47, 50, 52, 56, 61, 62]. All are abundant species in

453 coastal pelagic ecosystems where swordfish are usually caught. Seven species of Myctophidae, two

454 species of Scopelarchidae and one species of Bathylagidae were present in this study, indicating that

455 swordfish forage frequently in mesopelagic waters.

456   A number of the most important swordfish prey species are found in or associated with the

457 DSL, including jumbo squid, *G. borealis* and *Gonatus* spp. squids, barracudinas, and Pacific hake

458 [124-130]. Other important prey, like *Abraliopsis* sp. and market squid, are more epipelagic. The

459 range of prey species eaten, in terms of both prey size and prey habitat, suggests that swordfish have

460 quite flexible foraging strategies.

461

Dietary variation in swordfish

463   The importance of several prey taxa varied in relation to swordfish body size, location, year

464 and, in some cases, differed between the first and second half of the fishing season. Jumbo squid,

465 *Gonatus* spp. and Pacific hake were all more important as prey for larger swordfish than for smaller

466 ones. At least in part, this may reflect the ability of larger swordfish to catch and eat large prey. These

467 results differ from those of [62] who did not find variability in diet by size in swordfish off western

468 Baja California.

469   Jumbo squid, *Gonatus* spp. and market squid were more important inshore (within the SCB)

470 while *G. borealis* and Pacific hake were more important offshore (beyond the SCB). These

471   differences probably reflect prey availability but more information is needed on distribution of

472   cephalopods and fish to confirm this.

473   Significant between-year variation in diet was also apparent. In general, this may reflect long-

474   term variation in swordfish preference, prey availability, prey distribution, and prey abundance, but

475   could also be related to changes in fishing locations. According to GII results, jumbo squid was more

476   important in swordfish diet from 2007-2010 than in 2011-2014, with Pacific hake being the most

477   important prey item in the latter period. However, GAM analysis shows a peak in jumbo squid for

478   2012, suggesting this species increased in dietary importance after 2010, once other factors are taken

479   into account. These results likely relate to the range expansion of jumbo squid that occurred during

480   the first decade of the 2000s and the subsequent decline to lower levels in 2010 in the CCLME [131].

481   A prolonged decline of jumbo squid landings was observed also in the Gulf of California after El

482   Niño (2009-2010) and was associated with chronic low-wind stress and decreased chlorophyll a

483   [132].

484   *G. borealis*, *Gonatus* spp. and market squid were most important from 2008-2010, a period

485   which included both (cold) La Niña conditions in 2008 and a (warm) El Niño event in 2010. The

486   increased incidence of market squid in swordfish diet coincided with a high abundance of market

487   squid in both midwater trawl surveys and in landings [133]. The commercial squid fishery in

488   California targets spawning aggregations 1–3 km from the shore, around the Channel Islands and near

489   coastal canyons. Catches are highly influenced by El Niño events [134, 135]. The cooler water during

490   the La Niña years may have favored higher abundance and therefore higher catches in market squid

491   [136].

492   Northern anchovy is a monitored species under the Pacific Fishery Management Council's

493   Coastal Pelagic Species fishery management plan. It was only found in three stomachs in this study,

25

494   inside the SCB in 2007 and 2008. [61] examined the stomach contents of 15 swordfish caught near

495   the Southern California Channel Island in fall/winter of 1980 and found that northern anchovy

496   accounted for over 40% of IRI. These differences may be attributed to variations in anchovy

497   abundance over the years. Anchovy were present in higher numbers in the California Current prior to

498   1990 with a peak in catches around 1980 [137]. Catch estimates show that, starting around 2009 to

499   2013, northern anchovy biomass dropped to low levels [138]. Analysis of northern anchovy stock size

500   from 1951–2011 suggested that the population was near an all-time low from 2009–2011 [139], and

501   subsequent analysis suggested that the population remained low through 2015 [140]. More recent

502   minimum abundance estimates based on acoustic trawl surveys indicate the combined biomass of the

503   Northern and Central stocks rebounded to a range from 0.5 to 1.1 million metric tons in 2018 and

504   2019 [141, 142].

505   Pacific sardine (the abundance of which until recently was believed to vary inversely with that

506   of anchovy) [143-145] was not present in the diet in 2007 and sardine %F was low for other years of

507   the study. These results are possibly related to the low sardine biomass during the study period [146],

508   but they could be explained also by limited swordfish preference for sardine. [62] reported a low %F

509   for sardine in the diet of swordfish from northern Baja California in 1992-1993, a period when sardine

510   biomass was higher in the area.

511   Future diet studies on swordfish in the CCLME would benefit from more information on prey

512   distribution and abundance (and thus their availability to swordfish) and on the size distribution of

513   available and consumed prey. This would potentially allow elucidation of (multivariate) functional

514   responses (i.e., how numbers of a prey species in the diet relate to its abundance and the abundance of

515   other prey species) [147]. The present study would have benefited from a larger sample size since the

516   rarefaction curve (for number of prey species detected versus sample size) did not reach an asymptote.

517   Samples used in this study were collected during the fall/winter period and were fisheries-dependent

518   so information on the diet at other times of the year is lacking. Results are also potentially influenced

519   by the distribution and targeting of fisheries effort and catch. While additional studies are warranted,

520   this study provides the most comprehensive view of swordfish diets in the CCLME to date, allowing

521   for comparisons of diet in relation to size, year and area.

522

523   Supporting information

524   **Table S1.** Quantitative prey composition of the broadbill swordfish (EFL < 165 cm) in the California

525   Current. A total of 148 stomachs containing food was examined. Prey items are shown by decreasing

526   GII value. See methods for description of the measured values.

527   **Table S2.** Quantitative prey composition of the broadbill swordfish (EFL $\geq$ 165 cm) in the California

528   Current. A total of 140 stomachs containing food was examined. Prey items are shown by decreasing

529   GII value. See methods for description of the measured values.

530   **Table S3.** Comparison of GII for the main prey species between small and medium broadbill

531   swordfish. Values of mean GII, bootstrapped 95% CIs and % bootstrap runs in which each prey type

532   was in the smaller of two size categories of swordfish. If more than 95% (or fewer than 5%) of runs

533   show the prey type was more important in the smaller size category of swordfish than in the larger

534   category, we consider the difference to be significant. S = small (EFL < 165 cm), M = medium (EFL

535    $\geq$ 165 cm). These results are generally consistent with inferences from non-overlap of 95% CIs.

536   **Table S4.** Quantitative prey composition of the broadbill swordfish within the SCB subregion. A total

537   of 199 stomachs containing food was examined. Prey items are shown by decreasing GII value. See

538   methods for description of the measured values.

539 **Table S5.** Quantitative prey composition of the broadbill swordfish beyond the SCB subregion. A

540 total of 93 stomachs containing food was examined. Prey items are shown by decreasing GII value.

541 See methods for description of the measured values.

542 **Table S6.** Comparison of GII for the main prey species between broadbill swordfish within and

543 beyond the SCB region. Values of mean GII, bootstrapped 95% CIs and % bootstrap runs in which

544 each prey type was in each of two categories of swordfish. If more than 95% (or fewer than 5%) of

545 runs show the prey type was more important in one region than the other, we consider the difference

546 to be significant. East = within the SCB subregion, West = beyond the SCB subregion. These results

547 are generally consistent with inferences from non-overlap of 95% CIs.

548 **Table S7.** Quantitative prey composition of the broadbill swordfish during year 2007 in the California

549 Current. A total of 47 stomachs containing food was examined. Prey items are shown by decreasing

550 GII value. See methods for description of the measured values.

551 **Table S8.** Quantitative prey composition of the broadbill swordfish during year 2008 in the California

552 Current. A total of 16 stomachs containing food was examined. Prey items are shown by decreasing

553 GII value. See methods for description of the measured values.

554 **Table S9.** Quantitative prey composition of the broadbill swordfish during year 2009 in the California

555 Current. A total of 37 stomachs containing food was examined. Prey items are shown by decreasing

556 GII value. See methods for description of the measured values.

557 **Table S10.** Quantitative prey composition of the broadbill swordfish during year 2010 in the

558 California Current. A total of 12 stomachs containing food was examined. Prey items are shown by

559 decreasing GII value. See methods for description of the measured values.

560   **Table S11.** Quantitative prey composition of the broadbill swordfish during year 2011 in the

561   California Current. A total of 54 stomachs containing food was examined. Prey items are shown by

562   decreasing GII value. See methods for description of the measured values.

563   **Table S12.** Quantitative prey composition of the broadbill swordfish during year 2012 in the

564   California Current. A total of 36 stomachs containing food was examined. Prey items are shown by

565   decreasing GII value. See methods for description of the measured values.

566   **Table S13.** Quantitative prey composition of the broadbill swordfish during year 2013 in the

567   California Current. A total of 56 stomachs containing food was examined. Prey items are shown by

568   decreasing GII value. See methods for description of the measured values.

569   **Table S14.** Quantitative prey composition of the broadbill swordfish during year 2014 in the

570   California Current. A total of 34 stomachs containing food was examined. Prey items are shown by

571   decreasing GII value. See methods for description of the measured values.

572   **Table S15.** Comparison of GII for the main prey species for broadbill swordfish by year group.

573   Values of mean GII, bootstrapped 95% CIs and % bootstrap runs in which each prey type was in each

574   of two categories of swordfish. If more than 95% (or fewer than 5%) of runs show the prey type was

575   more important in one year than the other, we consider the difference to be significant. Y1 = Year1

576   (2007), Y2 = Year2 (2008-2010), Y3 = Year3 (2011-2014). These results are generally consistent

577   with inferences from non-overlap of 95% CIs.

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Acknowledgements

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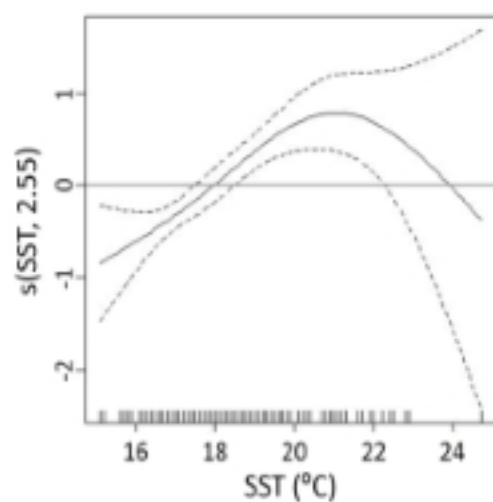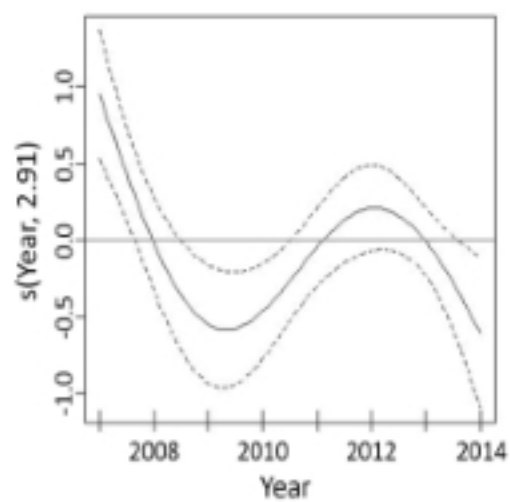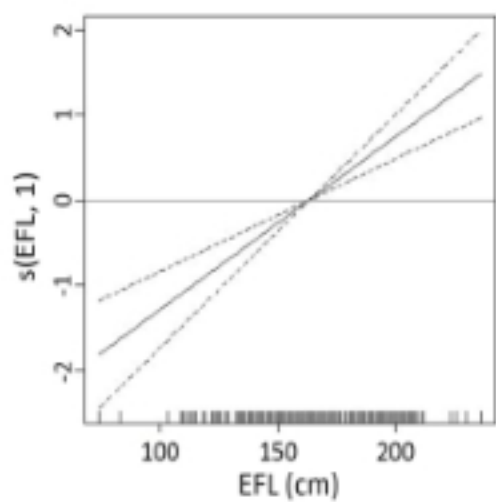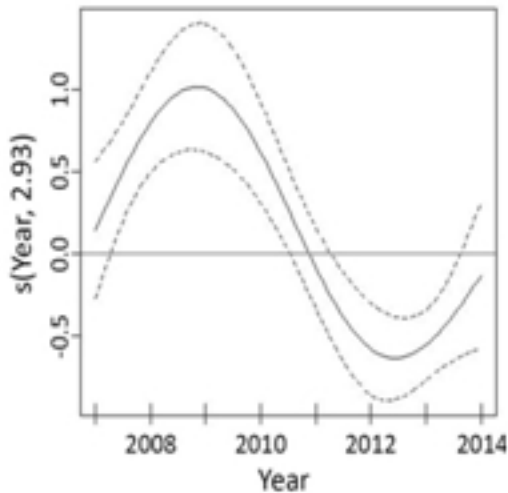
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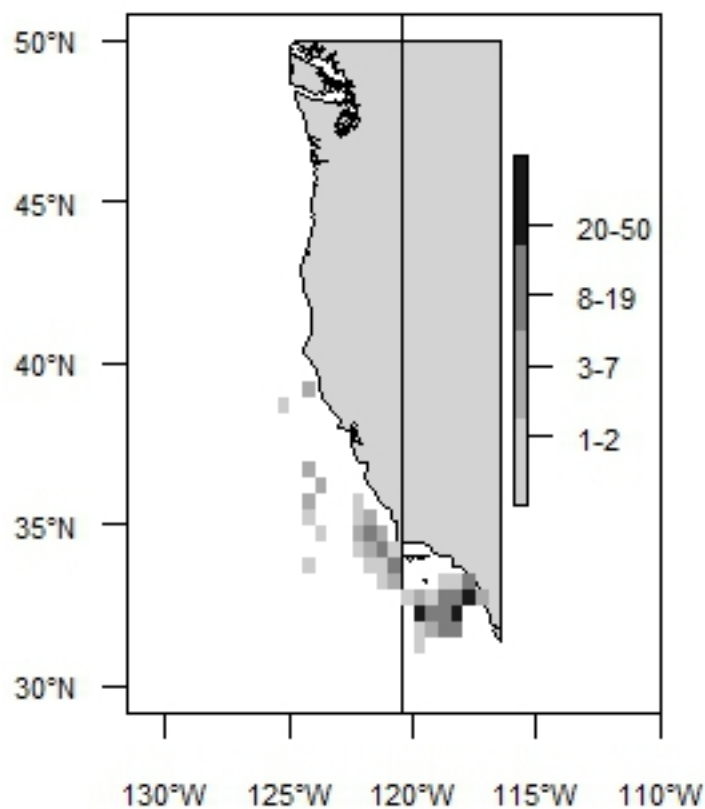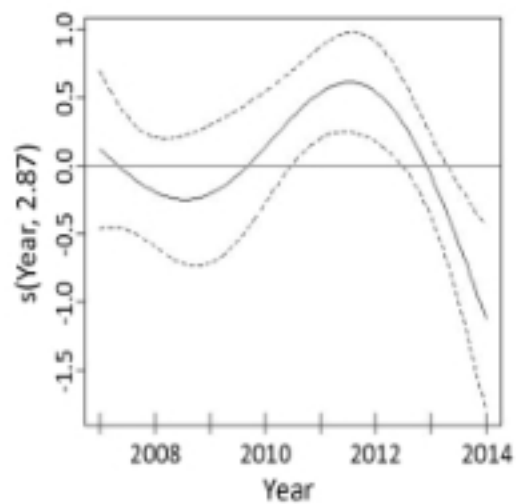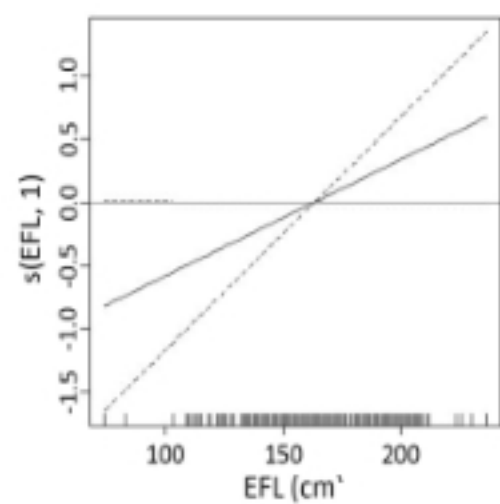
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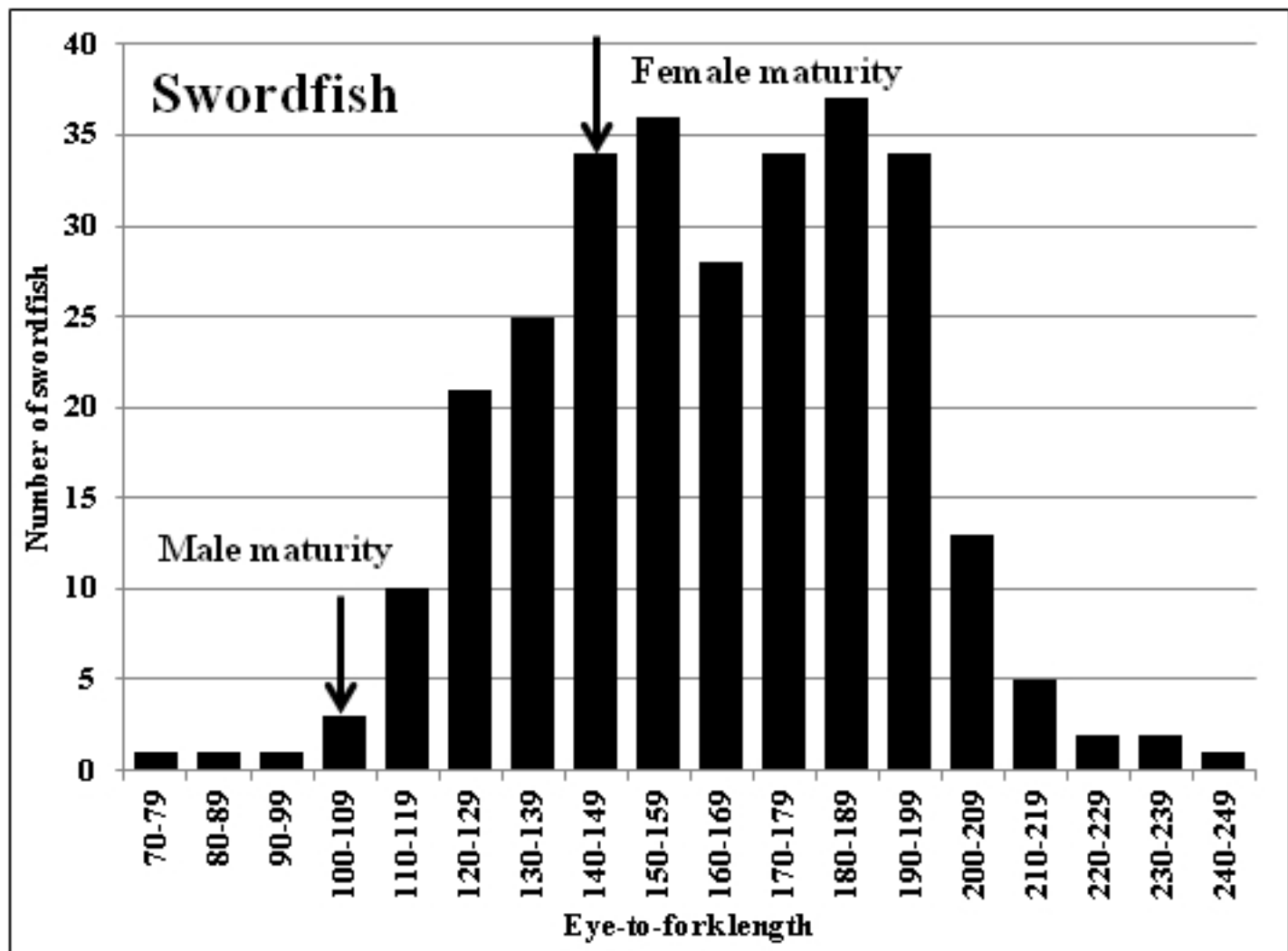
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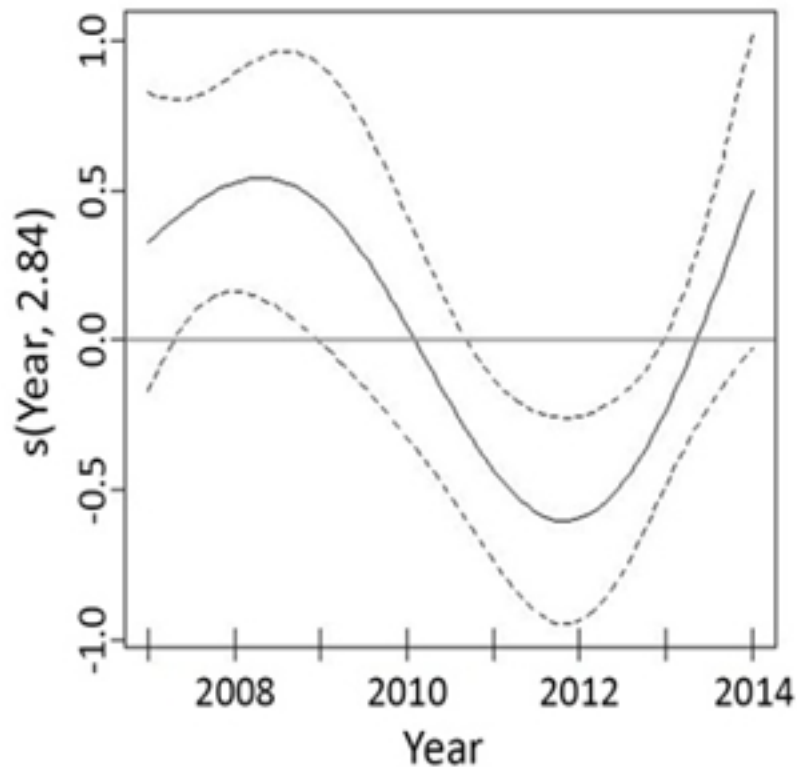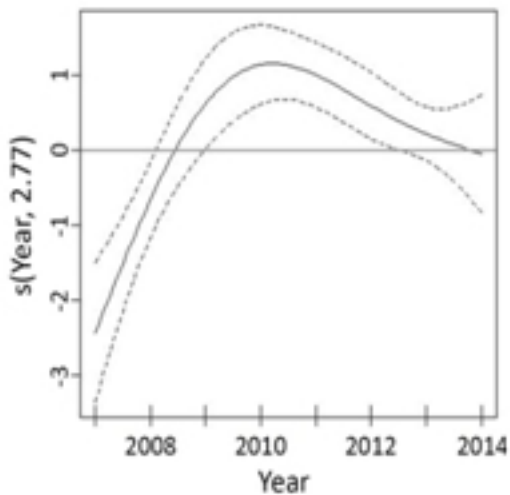
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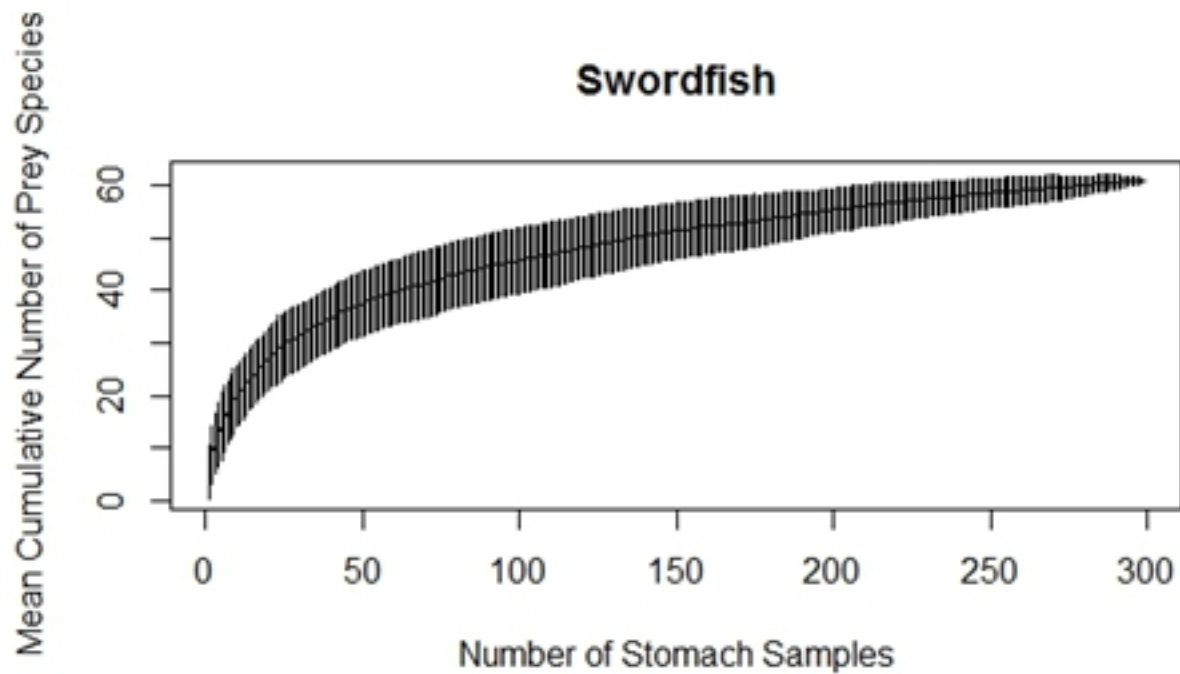
Figure

a. Jumbo squid

Figure

b. Gonatopsis borealis
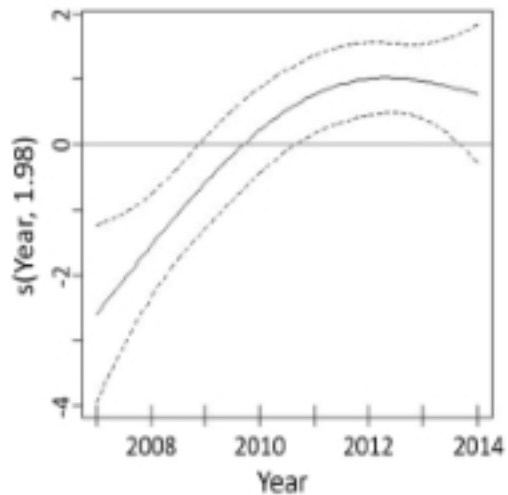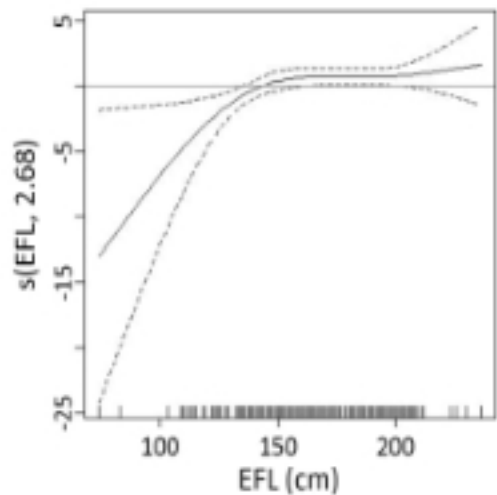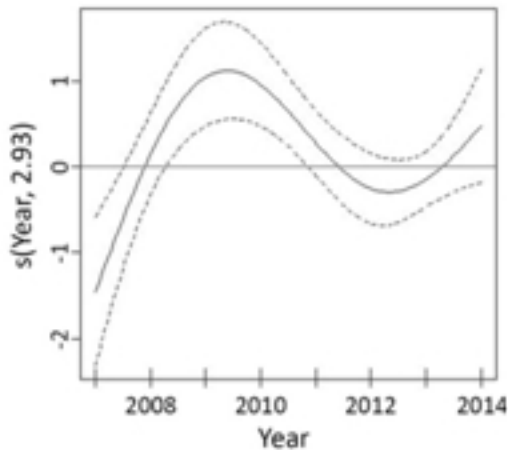
Figure

c. Abraliopsis sp.

Figure

d. *Gonatus* spp.

Figure

e. Market squid

Figure

f. Pacific hake

Figure

g. Duckbill barracudina

Figure