Responses of the northern anchovy to the dynamics of the pelagic environment: identification of fish behaviours that may leave the population under risk of overexploitation

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Northern anchovy *Engraulis mordax*, in an upwelling area off the west coast of Baja California, Mexico, had several strategies in response to chlorophyll *a* distribution and availability. When the pigment was scarce, northern anchovies practically disappeared from the area and they returned to coastal waters when it was abundant. The fish gathered in specific areas where low turbulence mixing and high concentrations of chlorophyll *a* existed. The northern anchovies, responding to food concentration in a stable environment, were probably vulnerable to over-exploitation because they were highly concentrated. More than 80% of the total fish density, estimated by acoustics, was recorded in a reduced area. Northern anchovies may have been vulnerable to the purse-seiner fleet because they were swimming at shallow depth; they were close to shore not far from the fleet's base and they were concentrated in an area where several fishing boats could catch them. Studying the responses of shoaling fishes to fluctuation in the pelagic environment, with the intention of identifying behaviours that may leave the stock highly vulnerable to fishing, may help guide their management. © 2004 The Fisheries Society of the British Isles

Key words: chlorophyll *a*; fishery management; fish shoaling behaviour; northern anchovy; upwelling.

INTRODUCTION

Pelagic fishes living in coastal waters are confronted with large variations in the pelagic environment that occur over different time scales and at different locations (Alongi, 1998). This is particularly evident in upwelling areas where marked seasonal and local variability exists (Huyer, 1983; Hutchings *et al.*, 1995). Besides heterogeneity in space and time, coastal upwelling ecosystems are highly dispersive environments, where eggs and larvae tend to be swept away from the highly productive areas (Bakun, 1996; Roy, 1998). A relatively small number of similar species, such as sardines and anchovies, have solved the problems of feeding, reproducing and growing in this environment. This has been done by adopting an arrangement of behavioural strategies designed to increase survival, *e.g.* plasticity in feeding, seasonal migrations, selection of

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suitable habitats for spawning and shoaling behaviour (O'Connell, 1972; Mais, 1977; Pitcher, 1986; Fowler & Boyd, 1998). The success of these strategies may be defined in terms of biomass (Blaxter, 1985). Populations of sardines and anchovies are well known to be able to support commercially important fisheries. Their populations, however, are notoriously variable. Large fluctuations in population densities have been documented long before fishing could be a factor (Soutar & Isaacs, 1974), and when fished, the catch can be quite substantial but unstable (Lluch-Belda *et al.*, 1989). One such example is the northern anchovy *Engraulis mordax* Girard stock, whose catch in north-west Mexico has been in steady decline since peaking at 258 000 t in 1981, with no recovery since its lowest catch of 99 t in 1990 (Garcia & Sanchez, 2002). A significant overall reduction in fishing activity would be the most complete and immediate approach to rebuild the stock. The stock assessment methods employed currenly and before the collapse, *i.e.* technical measures based on total landings, length and age-at-catch and fishing effort (Garcia & Sanchez, 2002) also need to be reviewed. Effective stock assessment and fishery management should also include a comprehensive understanding of fish behaviours that may influence vulnerability (Pitcher, 1995; Freon & Misund, 1999).

The objective of the present study was to investigate the responses of the northern anchovy to the dynamics of the pelagic environment in the upwelling area of the west coast of Baja California, Mexico. In particular, the responses of the northern anchovy to the variation of chlorophyll *a* both in time and space. *Engraulis mordax* is a planktivorous organism (Loukashkin, 1970), and on the west coast of Baja California phytoplankton may occupy >55% of individual items in the stomach contents (Chiappa & Gallardo, 1993). The current status of the population allows the behaviour of northern anchovies to be studied in a depleted situation that might contrast with future stock size. Population growth in the following years is expected because fishing mortality on this species is now at its lowest level. Currently, the fishing fleet is targeting other species such as the Pacific sardine *Sardinops sagax* (Jenyns) and Pacific mackerel *Scomber japonicus* Houttuyn, and occasionally the northern anchovy is captured (Garcia & Sanchez, 2002).

THE STUDY AREA

The study area was within the fishery operations of the purse seine fleet based in Ensenada, Mexico. It is characterized by the presence of active coastal upwelling sites (Hutchings *et al.*, 1995), as recorded by *in situ* fluorescence and water temperature, which vary in intensity and locations during the year. The study area was within the boundaries of the California Current System (CCS). This is an eastern-ocean coastal upwelling system where the dominant flow is the California Current (CC) carrying low salinity and low-temperature waters towards the equator (Lynn & Simpson, 1987). Below the CC is the California Undercurrent (CUC) flowing poleward over the continental slope and identified by its warm, saline, low-oxygen and nutrient-rich waters coming from the eastern equatorial Pacific (Hickey, 1979). A third flow, known as the Inshore Current or Davison Current (DC), is a relatively weak surficial, poleward flow. Some studies suggest that the DC is a result of the CUC shallowing

(moving to the surface) in the late autumn when the CC is weakest (Huyer & Smith, 1974). The CCS is influenced by large-scale wind forcing, where the most obvious scale of variation is seasonal. Off the northern west coast of Baja California, the winds towards the equator are favourable for upwelling year-round; however, the strongest wind-driven upwellings occur from March to June, diminishing from September to December (Bakun & Nelson, 1977).

MATERIALS AND METHODS

From 26 to 30 November (autumn) 2000 and 25 to 29 March (spring) 2001 on board the R/V El Puma (50 m long), seven 28 km transects separated by an average of 32 km were sampled off the north-west coast of Baja California from Punta Colnett to Punta San Fernando (30°90′ N to 29°43′ N and 115°48′ W to 116°66′ W) (Fig. 1). The study area from north to south covered *c.* 220 km of coast line. Four oceanographic stations were established along each transect. Each transect was intended to cover three areas, each *c.* 9 km long. The oceanic area, between stations one and two, was the deepest (depth >1000 m) and was in the offshore part of the transect. A slope area, between stations 2 and 3, covered all the shelf break (depth range ± 200 m). A neritic area, between stations 3 and 4, covered the shallower part of the transect (depth <80 m).
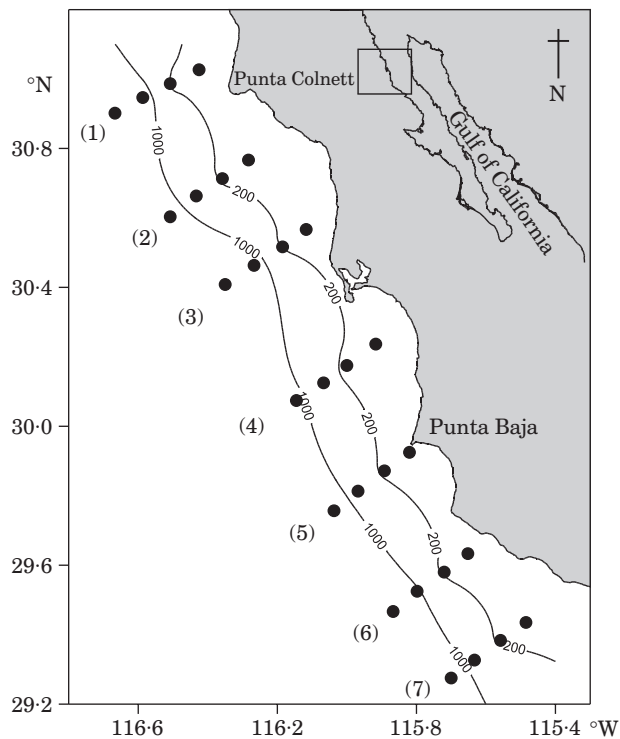

FIG. 1. Map of study area. Transect number is given in parentheses with sampling stations (●). ⸺⸺, 200 and 1000 m isobaths.

SAMPLING PROTOCOL

Cruises started at the oceanic station of transect 1 (station one), headed towards station 2, and arrived at station 4 $c.$ 4 h later. At each station, temperature and salinity along the water column were recorded using a General Oceanics Mark III CTD. Water samples were taken with Niskin bottles at 5, 10, 15, 20, 25, 30, 40 and 50 m depth to measure fluorescence. Water samples were kept in the dark until measured. Fluorescence was measured using a Turner Designs 10-AU-005-CE fluorometer (excitation 340–500 nm, emission >665 nm). Raw fluorescence data were recorded in the field and the records were calibrated with laboratory measurements of standard chlorophyll a (chl-a) provided by Turner Designs. Results are reported as µg chl-a l^{-1}. All the fluorescence samplings were done during daylight between 1000 and 1600 hours local time. Field fluorescence data were converted to chl-a using the regression equation: chl-a (µg l^{-1}) $= 0.119 + 0.0072$ field fluorescence data ($r^2 = 99.6$, $n = 55$, $P < 0.0001$; Robinson *et al.*, 2004*a*, *b*). Wind speed and direction was recorded at each station.

HYDROACOUSTICS

Acoustic data were collected using a SIMRAD EY-500 split-beam echosounder connected to a SIMRAD 120 kHz, 3.5×3.5 degree transducer mounted at 4 m depth on the keel of the ship. Pulse duration was set at 0.3 ms. Ping rate averaged 1.3 pings s^{-1} and power output was 63 W. The echosounder was calibrated with a standard 23 mm copper sphere (-40.4 dB). The calibration sphere was suspended under the vessel and calibrated using the procedure described in the SIMRAD EY-500 instruction manual (SIMRAD, 1998). For analysis, the SIMRAD EP500 Echo Processing (EP) System, ver. 5.3 (SIMRAD, 1997) was used. This is an echo-counting analysis system that transforms the received echo distribution into area densities and hence abundance estimates. The system has the capability of digitizing and storing hydroacoustic transects. Analysis of echo counting included both single target-strength analysis (TS) and TS size distribution. Results for echo counting are given as individuals per hectare (ind. ha^{-1}). Transects 2, 4 and 6 were surveyed only during the day. In transects 1, 3, 5 and 7, after the four oceanographic stations were done, the ship continued surveying the transect through the night until 0600 hours. Echograms were generated as each area was surveyed. Ship speed along the transect averaged 18.5 km h^{-1} (10 knots). Only echograms gathered from 2000 to 0500 hours were analysed. This was done to ensure complete darkness because small pelagic fishes such as the northern anchovy disperse over the water column during the night enabling echo counting (Robinson *et al.*, 1995). Analysis of each echogram was limited from 10 to 50 m depth (in shallow areas, 5 m above the bottom). Echograms were divided (depth 10–30 m; depth 30–50 m), and echo counting was made for each layer.

The length-at-capture of the northern anchovy by the Ensenada fleet ranges from 9 to 15 cm total length (L_T). This represents an age of 5 months to 2 years (Sakagawa & Kimura, 1975). On the basis of this range, the length-target strength was calculated assuming the relation TS $= 20 \log_{10} L_T + b_{20}$ (MacLennan & Simmonds, 1992). For the intercept constant (b_{20}), a value of -73.1 dB was used following the results obtained by Dengbol *et al.* (1985), who worked with a 120 kHz frequency on mixed herring *Clupea harengus* L. and sprat *Sprattus sprattus* (L.). Accordingly, the 9–15 cm L_T represents TS values between -54 and -49.5 dB. From the 3 dB target-strength class division provided by SIMRAD EP (SIMRAD, 1997), a range of -53 to -48 dB was used.

MIDWATER NET SAMPLING

Isaacs-Kidd midwater trawls were deployed in transects 1, 3, 5 and 7 (night). The net had a 2.8×2.8 m mouth and 12.7 mm stretch mesh with a plankton-bucket attached at the codend. There was no systematic sampling as was done for the oceanographic data. The net was deployed at depth and in the area where echosounder information, displayed on the computer screen in real time, showed the presence of echoes related to small pelagic fishes. Towing speed was 9.25 km h^{-1} (5 knots). A Sea-Bird CTD was attached to the net to determine trawling depth.

RESULTS

WIND SPEED AND DIRECTION

Winds were from the north-west (310–320°) during both seasons. Wind speeds recorded in March were typically strong and twice the speed recorded in November (median November $7 \cdot 5 \, \text{m s}^{-1}$; median March $14 \cdot 5 \, \text{m s}^{-1}$; Mann–Whitney test, $P < 0 \cdot 05$).

SEA TEMPERATURE AND SALINITY AT 10 M DEPTH

Sea temperature in November ranged from $14 \cdot 1$ to $17 \cdot 6°$ C, dropping significantly during March, which ranged from $12 \cdot 0$ to $15 \cdot 7°$ C (ANOVA, $P < 0 \cdot 0001$, $n = 28$) [Fig. 2(a)]. During both surveys, temperature distribution had a traditional upwelling-type structure with cold temperatures near the coast. In November, however, isotherms ran to the coast indicating a poleward intrusion of warm water (Gammelsrod *et al.*, 1998). During the autumn, there were two zones with temperatures below the isotherm of $15°$ C. These two zones were divided by an intrusion of warm water recorded in the oceanic area in transects 2 and 3. By spring, cool temperature was more or less continuous along the coast as a result of the temperature front created by the upwelling process (Cole & McGlade, 1998), except in the southern part where the $15°$ C isotherm was close to the shore [Fig. (2a)]. Salinity was high during autumn, ranging from $33 \cdot 57$ to $33 \cdot 74$. Salinity decreased during spring, ranging from $33 \cdot 47$ to $33 \cdot 82$ (ANOVA, $P < 0 \cdot 001$, $n = 28$) [Fig. (2b)]. During November, salinity showed two areas with high values in the oceanic part of transect 2 and 3 and near the coast in transect 7. In March, there was an oceanic-neritic pattern, with high salinity near the coast [Fig. (2b)].

DISTRIBUTION OF VERTICAL TEMPERATURE ALONG TRANSECTS

Water temperature along transects was plotted for transects 1, 3, 5 and 7 (Fig. 3). Overall during both months, isotherms rose towards the surface from deep oceanic waters, indicating coastal upwelling processes. During spring, the formation of steep surface fronts in transect 1 and transect 5 was noticeable, resulting in a strong horizontal gradient of temperature where mixing and diffusion may occur (Frank, 1992).

CHLOROPHYLL *a*

During autumn, chl-*a* ranged from $0 \cdot 60$ to $0 \cdot 76 \, \mu\text{g} \, \text{l}^{-1}$ and by spring chl-*a* bloomed to values ranging from $0 \cdot 51$ to $5 \cdot 64 \, \mu\text{g} \, \text{l}^{-1}$ (ANOVA, $P < 0 \cdot 001$, $n = 28$, pooling all records for each month). During November, chl-*a* was homogenously distributed in the area [coefficient of variation $(CV) = 8 \cdot 4\%$; χ^2, $P > 0 \cdot 05$, comparing relative distribution to the theoretical expected frequencies]. During March, chl-*a* distribution in the area was more heterogeneous ($CV = 63 \cdot 3\%$; χ^2, $P < 0 \cdot 10$).

For both surveys, high values of chl-*a* were concentrated in a narrow range of water temperature measured from 5 to 50 m depth. During autumn, chl-*a* was
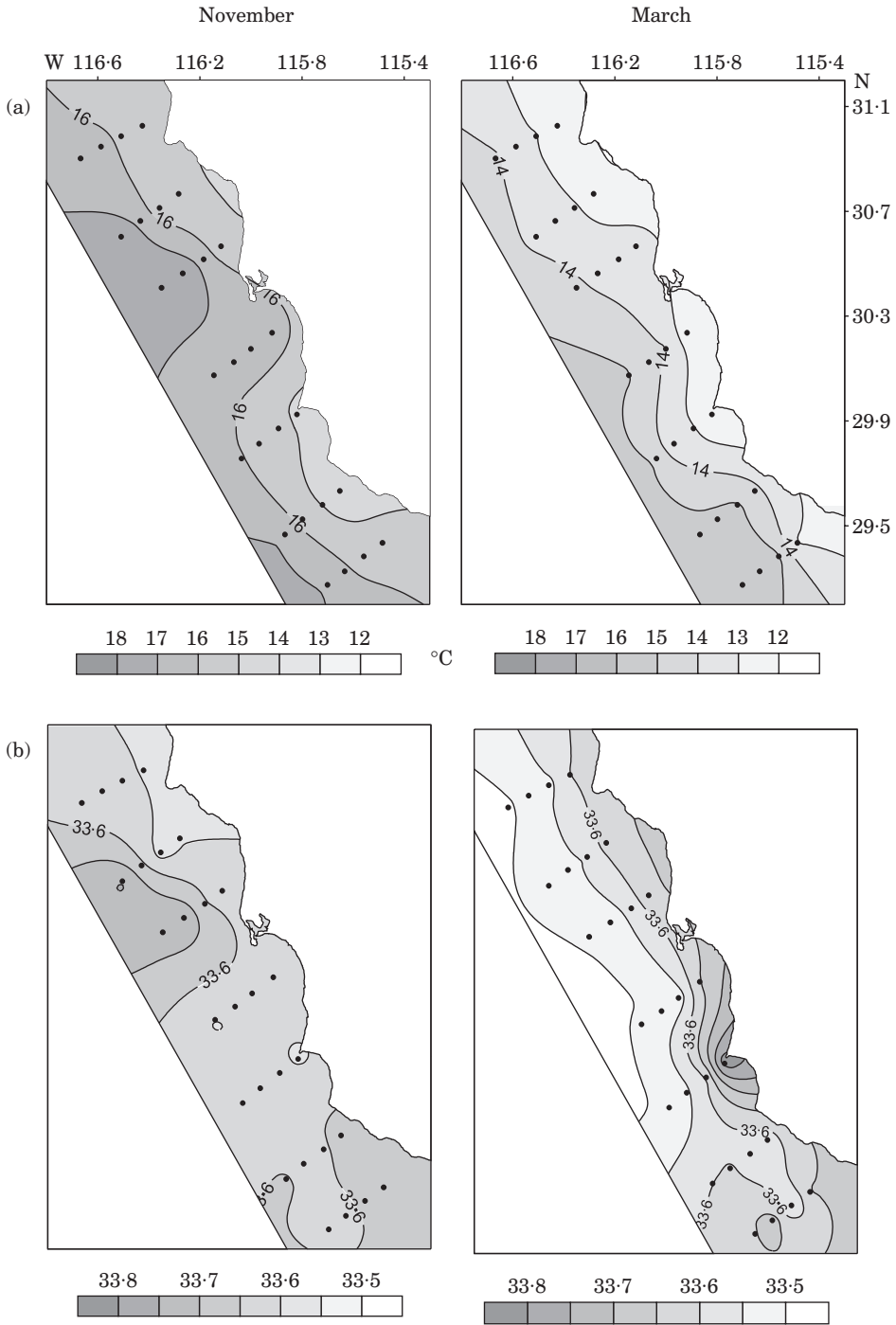
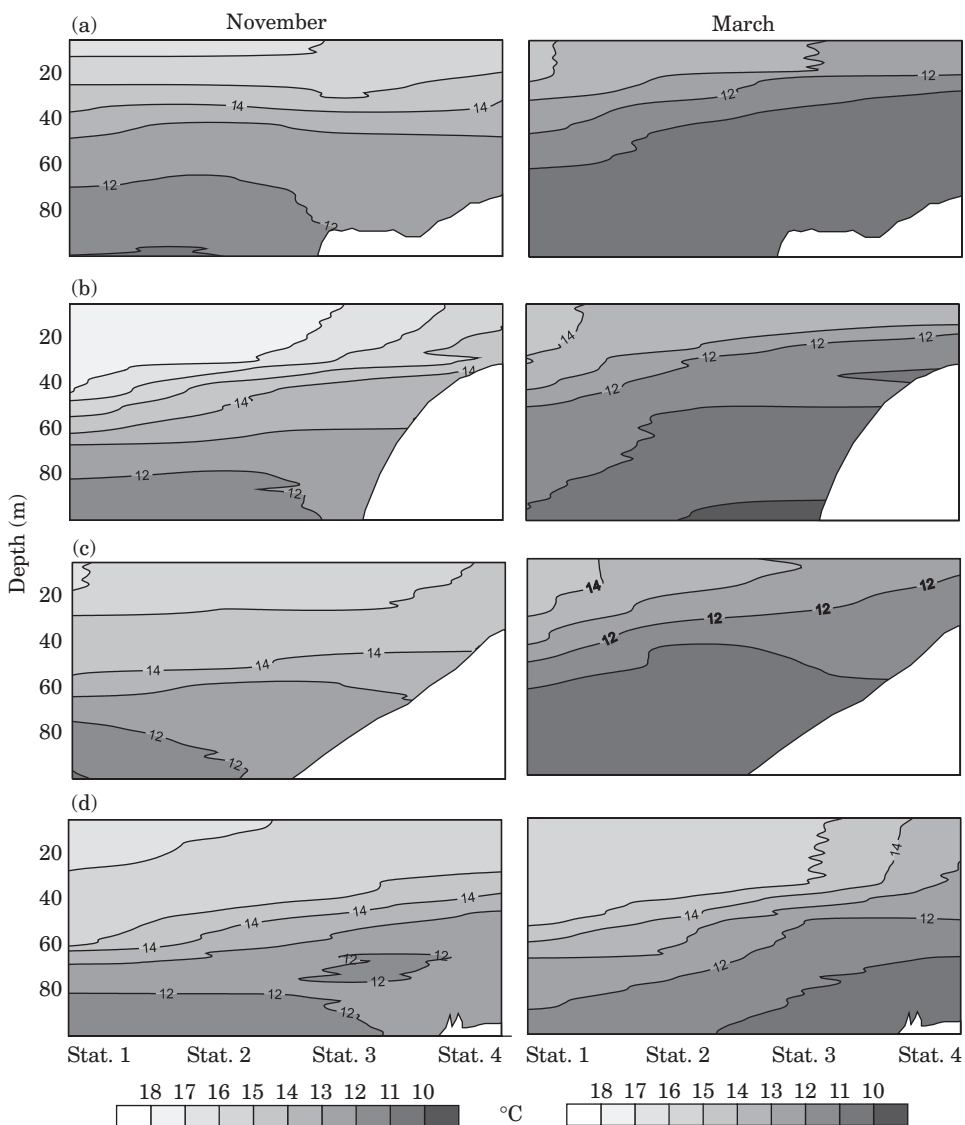FIG. 2. Contours at 10 m depth of (a) temperature and (b) salinity.

FIG. 3. Vertical profiles in November and March of temperature along transects (a) 1, (b) 3, (c) 5 and (d) 7 (see Fig. 1).

high at *c*. 15° C [Fig. (4a)], and by spring, the pigment was concentrated at *c*. 13° C [Fig. (5a)]. Distribution of the pigment was bell-shaped for both surveys.

The oceanic and outer shelf chl-*a* maximum was deepest in November (median November 30 m depth; median March 15 m depth; Mann–Whitney confidence interval test, $P = 0.02$). This difference, however, was not significant in the neritic stations, and during March the maximum fluorescence was found deep in the southern transect in the oceanic and shelf-break stations.

Chl-*a* values were integrated along the water column (5–25 m) (Fig. 6). During November, the pigment was high towards the coast, with two areas
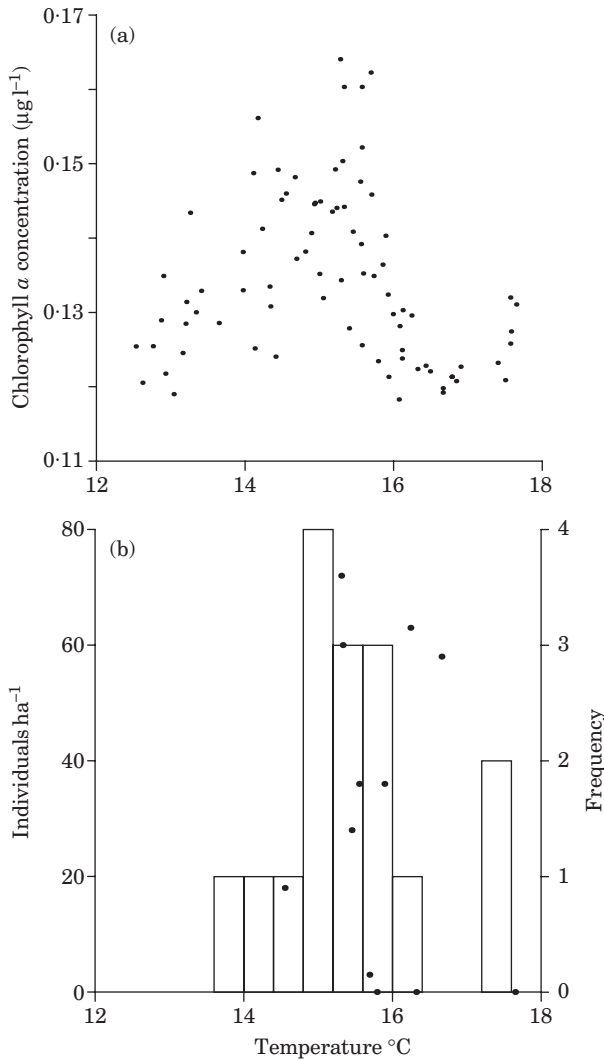
FIG. 4. (a) Distribution pattern of chlorophyll *a* with temperature obtained during November. Multiple depth-specific observations (5–50 m depth) from individual stations are plotted independently. (b) Median fish density (●) and frequency distribution of temperature at 25 m depth (□) for November.

of concentration in the neritic area of transects 1, 2 and 3 and in the neritic and slope area of the southern transects. During March, integrated values of chl-*a* showed three zones with high concentration: the neritic area of transect 1, the slope and neritic areas of transects 2 and 3, and the slope area of transect 5.

HYDROACOUSTICS

During November fish density in the study area ranged from 2 to 256 ind ha^{-1} ($CV = 97\%$), and by March the range increased from 2 to 8370 ind ha^{-1} ($CV = 367\%$). The sum of fish densities was far greater during March (November
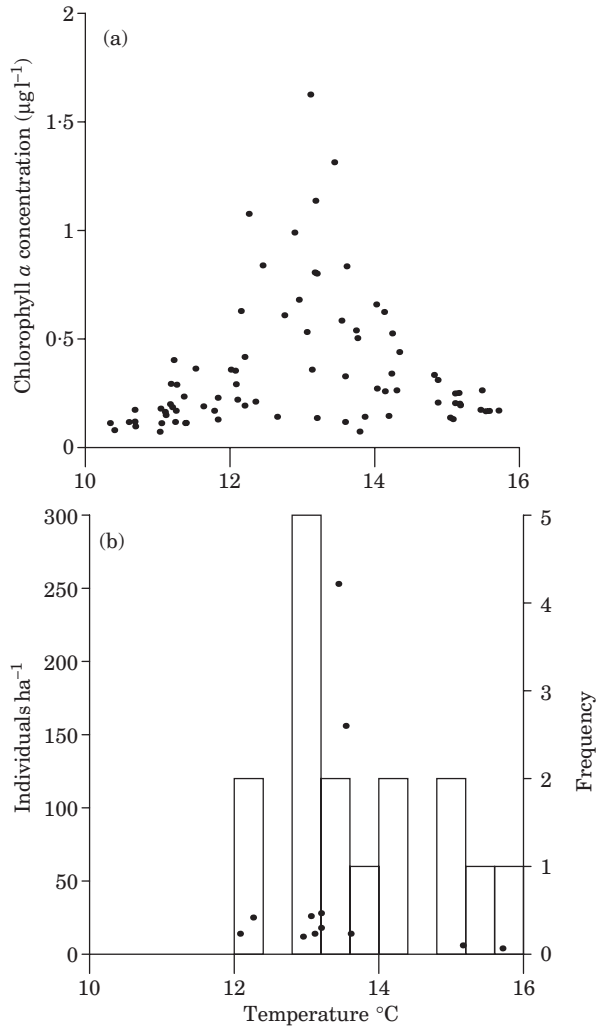
FIG. 5. (a) Distribution pattern of chlorophyll *a* with temperature obtained during March. Multiple depth-specific observations (5–50 m depth) from individual stations are plotted independently. (b) Median fish density (●) and frequency distribution of temperature at 25 m depth (□) for March.

sum $= 2496$ ind ha^{-1}, number of echograms 69; March sum $= 22\,343$ ind ha^{-1}, number of echograms 56); however, there was no significant difference in the medians (median November 46 ind ha^{-1}; median March 26 ind ha^{-1}, Kruskal–Wallis test, $P = 0.13$). During November the frequency distribution of fish density (ln transformed) was unimodal ($P < 0.05$). In March, the frequency distribution showed a distribution of high fish density not observed during November.

During November, most of the echoes were found in the southern transect, but no significant difference in fish density between transects was found (Kruskal–Wallis test, $P = 0.25$), nor were differences within areas (Kruskal–Wallis test, $P = 0.16$) (Table I). During March, fish density between transects was significantly different (Kruskal–Wallis test, $P = 0.001$). More than 80% of the echo
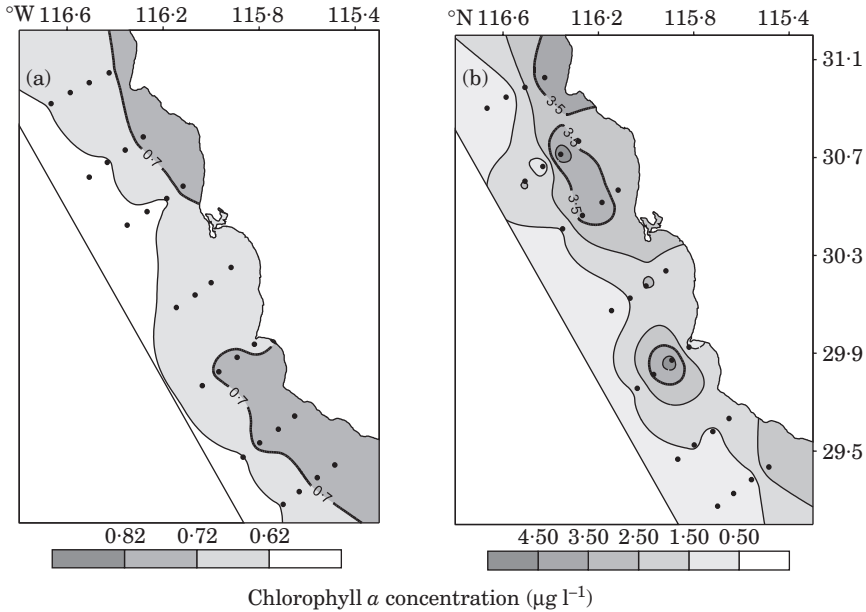
FIG. 6. Contours of chlorophyll *a* integrated from 5 to 25 m depth in (a) November and (b) March.

counting was obtained in transect 3 alone, but there were no differences within areas (Kruskal–Wallis test, $P = 0.16$) (Table I).

Results show that for November most of the abundance was found in the deeper layer (median shallow layer $= 31$ ind ha^{-1}, median deep layer $= 83$ ind ha^{-1} Mann–Whitney test, $P < 0.05$). In March, both layers were equally dense (median shallow layer $= 28$ ind ha^{-1}; median deep layer $= 26$ ind ha^{-1} Mann–Whitney test, $P < 0.05$). When the analysis was applied only to transect 3, where most of the abundance was found, however, most of the fish density was found in the upper layer (median shallow layer $= 360$ ind ha^{-1}; median deep layer $= 67$ ind ha^{-1} Mann–Whitney test, $P < 0.05$).

ECHO COUNTING RELATED TO TEMPERATURE AND CHL-*a* DISTRIBUTION

For each survey, fish density, depth 5–50 m, was plotted against sea temperature and chl-*a*. Because echo counting was the result of surveys between stations, median fish density was plotted against temperature recorded at the station closer to the shore. For instance, acoustic data gathered between stations 1 and 2 were plotted against temperature obtained at station 2 and so on. The fish density data used for the plots are presented in Table I. For November the relation was plotted against temperature at 25 m depth. For March, it was plotted against temperature at 10 m depth. During November, most of the abundance was found between 15 and 17° C, close to the range where the highest chl-*a* was recorded [Fig. (4b)]. During March, most of the abundance was found near 13° C, which is also close to the temperature where most of the pigment was found [Fig. (5b)].

TABLE I. Fish density (ind ha^{-1}) obtained from echo counting. Numbers are medians with the first and third quartiles in parentheses. n, number of echograms analysed. No data means no echoes within the selected target strength (TS) range

Transect	Oceanic	Shelf	Neritic	All the transect
November				
1	0 (no data)	0 (no data)	0 (0–0)	0 (0–0)
n	6	6	6	18
3	0 (no data)	0 (0–0)	72 (65–77)	72 (60–76)
n	6	6	6	18
5	36 (13–104)	36 (20–91)	18 (7–29)	30 (13–77)
n	5	5	5	15
7	63 (5–182)	60 (25–235)	3 (2–60)	46 (5–159)
n	6	6	6	18
March				
1	18 (5–28)	26 (3–73)	25 (7–59)	27 (9–42)
n	2	2	2	6
3	14 (0–68)	253 (53–501)	156 (0–1534)	89 (34–575)
n	7	6	6	19
5	28 (0–5)	14 (5–32)	14 (10–21)	14 (6–30)
n	3	6	6	15
7	4 (2–344)	6 (1–45)	12 (7–58)	9 (2–40)
n	4	6	5	15

MIDWATER NET SAMPLING

A total of 25 trawls were made, with 12 in November and 13 in March. The mean depth of trawling was 22 m (range 8–32 m). The mean time of trawling was 38 min (range 15–60 min). In November, northern anchovy, was caught in transects 3 and 5 ($n=45$, mean $L_T=11 \cdot 1$ cm, range 8·5–12·5 cm and $n=15$, mean $L_T=9 \cdot 1$ cm, range 8·0–12·0 cm, respectively). Beside the northern anchovy, the Pacific sardine was also caught, but only in small quantities in transect 3 ($n=10$, mean $L_T=8 \cdot 6$ cm, range 7·5–9·3 cm). In March, the diversity of the catch increased. The northern anchovy was captured in transects 3 and 5 ($n=175$, mean $L_T=9 \cdot 1$ cm, range 8·5–10·3 cm and $n=20$, mean $L_T=8 \cdot 1$ cm, range 8·0–10·3 cm, respectively). Most of the capture in all trawls, however, were the pelagic red crab *Pleuroncodes planipes* ($n>1000$, mean standard caparace length $=17 \cdot 1$ mm) and Myctophidae ($n=725$, mean $L_T=4 \cdot 5$ cm, range 3·2–5·2 cm).

DISCUSSION

Northern anchovies demonstrated several responses to variation in chl-*a* distribution and availability. When the pigment was scarce, the northern anchovies practically disappeared from the area. They usually migrate to deeper waters offshore in winter (Kucas, 1986) and return to coastal waters during spring. Notwithstanding how much phytoplankton was in the area, the behaviour of northern anchovies during both surveys was rather similar; they were

abundant in areas where chl-*a* was abundant, both in the horizontal plane and at depth. During the spring, however, there was a constraint. The fish were scarce in locations where steep fronts occurred, even though fluorescence was high. The reason may lie in offshore transport and turbulence. Northern anchovy spawning occurs all year, but peaks in winter and spring (Stauffer & Parker, 1982). Eggs are pelagic and may be swept away from high-productivity areas by strong offshore transport and wind-driven turbulent mixing (Frank, 1992). Spawning fishes seem to avoid these areas (Parrish *et al.*, 1983), remaining in zones characterized by a large, flat, and not very deep continental shelf (Roy, 1998) as found in transects 2 and 3.

During November, fish density–frequency distribution was basically unimodal, contrasting with March where the frequency distribution of fish density showed two groups. Fish located outside the productive areas during March were found in a fish-density distribution similar to that found in November. Accordingly, it seems that those fish shared the same conditions; they were found in areas were food was scarce. This behaviour agrees with the theory that fishes confronted with a poorer environment would swim in small groups (Duffy & Wissel, 1988; Nonacs *et al.*, 1998), reducing food competition (Street *et al.*, 1984). During March, high fish density was recorded in a reduced area, a condition that can be supported only by highly productive waters (Koslow, 1981).

Engraulis mordax feeds on plankton, and off the west coast of Baja California phytoplankton is an important constituent of its diet. Zooplankton is the major contributor of carbon to its diet (Chiappa & Gallardo, 1993), however, reinforcing the finding that pelagic fish populations in upwelling areas may not be supported by direct feeding on phytoplankton (Monteiro *et al.*, 1991). In the present work, results indicate that abundance and distribution of northern anchovies may be related to variations in chl-*a*; however, analysis of the stomach contents suggests that fish may also be targetting phytoplankton grazers such as copepods and euphausiids (Chiappa & Gallardo, 1993).

IMPLICATIONS OF THE BEHAVIOUR IN THE FISHERY

The responses of the northern anchovy to the dynamics of the pelagic environment as described here may leave the population at risk of overfishing. First, they tend to become highly concentrated within small areas. More than 80% of the total fish density (as estimated by acoustics) was recorded in the neritic and shelf-break segments of transect 3. Second, they were accessible to the fishery. Northern anchovies were easy targets for the purse-seiner fleet because they were swimming at shallow depth not far from the fleet's base, and they were found in a reduced area where several fishing boats could catch them (Freon & Misund, 1999). This behaviour resembles that of the Peruvian anchoveta *Engraulis ringers* Jenyns during El Niño 1972–1973, when the spawners were concentrated near the coast, remaining vulnerable to the fishing fleet (Santander, 1980). Peruvian anchoveta catch increased during this period, and the stock then declined substantially as a result of low recruitment and overfishing.

Fishes dwelling in upwelling areas live in a rich but complex system (Summerhayes *et al.*, 1995). Their food is abundant, but is patchily distributed and subject to marked variations in time and space. Even at locations

characterized by a 'quasi-permanent' upwelling, there is considerable variation of nutrient supplies occurring over time scales of days to weeks (Hutchings *et al.*, 1995). In this environment, shoaling is a productive behaviour. In a patchy and unpredictable environment, reduction in search times may represent one of the most important benefits of grouping (Pulliam & Caraco, 1984). Individuals in a shoal have a greater chance to find food because there is an increase in the total visual field perceived by the group (Eggers, 1976). Confronted with this ephemeral and competitive environment, the fishes' response should be fast and voracious (Robinson, 1996). It is likely that more than a single group of fishes may locate the source of food. If this occurs, several shoals may gather in the area forming clusters (Freon & Misund, 1999) as was observed in the present study.

A sustained fishery involves the use of resources in such a way that it is not depleted or permanently damaged, and options for achieving sustainability require understanding of marine ecosystems (NRC, 1999). Recognition that responses of shoaling fishes to natural events may leave the stock vulnerable to fishing suggests that suitable harvest strategies and fishing tactics should be implemented. The problem with shoaling species is that their coming together facilitates fishing, making the fishes easy to catch, but difficult to manage (Pitcher, 1995). Moreover, introducing new strategies for exploiting shoaling fish species is not an easy task. Most of the studies on shoaling behaviour are directly or indirectly devoted to increasing capture and not to preserving fish populations (Parrish, 1999), and the techniques employed in the management of shoaling fish species are practically the same as those utilized for managing non-shoaling species (Hilborn & Walters, 1992).

The amount of fish harvested from the northern anchovy population in Mexico indicates that fishing obviously has an effect on the stock decline (Garcia & Sanchez, 2002). It is not known, however, to what extent the population collapses of small pelagic fishes are caused by fishing or environmental changes, since often both are important factors (Muck, 1989; Sharp & McLain, 1995). For instance, the spawning biomass of northern anchovy declined abruptly from 1975 to 1979, but catch and fishing effort never reached a level sufficient to explain the decline (Fiedler *et al.*, 1986). Studies of fish shoaling behaviour suggest that fishing not only reduces fish populations, but may also disrupt the natural advantages of shoaling, and thus indirectly reduce stock sizes. When a shoal is larger than the gear or the holding capacity of the boat, fishermen usually capture only parts of a shoal (Freon & Misund, 1999). In this case the situation of the remaining fish is known only; suddenly they swim in a smaller shoal. The shoal may remain smaller, but individuals may be left vulnerable to predation. The probability of any individual in a group being captured in a single predator attack decreases as group size increases (Hamilton, 1971; Morgan & Godin, 1985). The shoal may join another group, and here at least two situations may occur. First, food competition increases as group size increases (Street *et al.*, 1984). Second, shoal homogeneity (*e.g.* fish length and hunger level) (Robinson & Pitcher, 1989) may be altered, and the confusion effect against predator attack, one of the most powerful forces that promotes association in animals, may fail (Landeau & Terborgh, 1986). It is expected that shoaling fishes will resume swimming in groups tending to avoid these situations. It is not know, however, whether persistent fishing may alter this tendency.

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