Fisheries Oceanography
An Integrative Approach to Fisheries Ecology and Management

Edited by
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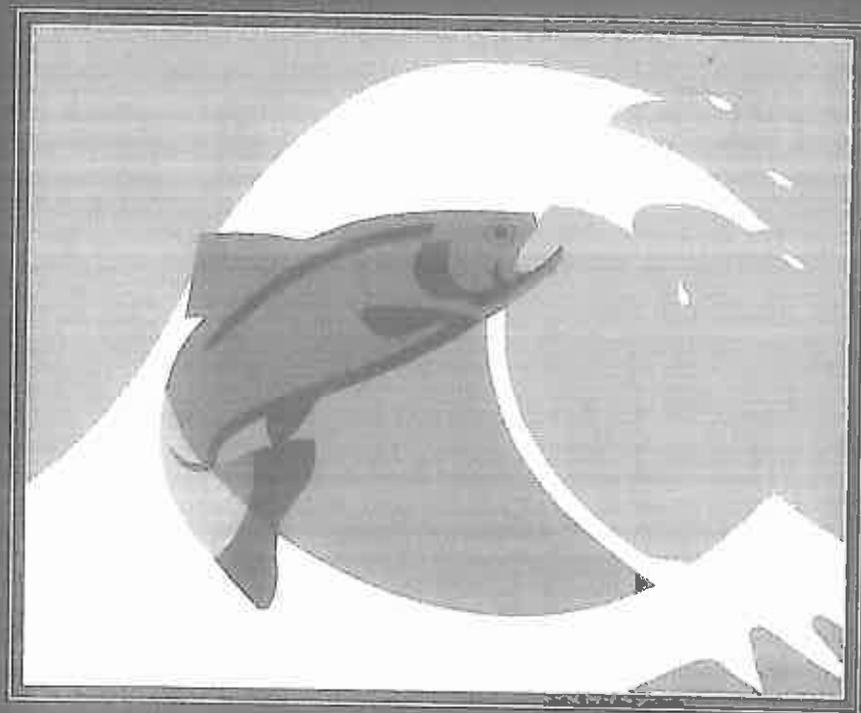
Chapter 2
Pelagic Fish Early Life History: CalCOFI Overview

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2.1 Introduction

The CalCOFI (California Cooperative Oceanic Fisheries Investigations) programme is a long-term study of the marine fish and environment in the eastern boundary of the North Pacific Ocean. It began in response to the disappearance of Pacific sardines from fisheries and habitats of 2000 km of coast off British Columbia, Washington, Oregon and northern California beginning in 1947. While major catches of sardines continued in the 1950s, from the southern California and northern Baja California habitats, the population was reduced to remnants in coastal waters in the 1960s. Descriptions of population biomass by Murphy (1966) and MacCall (1979) make it clear that the sardine population had been reduced by three orders of magnitude between the 1930s and the 1960s (Table 2.1). Recovery began in the late 1970s and the sardine population has recovered two orders of magnitude in the last two decades (Deriso *et al.*, 1996). The sardine population has now passed 2 million tons (Hanan pers. comm.1999) and occupies the Gulf of California, the entire coastline of the California Current and penetrates northward into coastal Gulf of Alaska (Ware pers. comm. 1999).

Eventual recruitment predictions from CalCOFI procedures will probably be based on northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*) and

Table 2.1 An abbreviated time history of order of magnitude changes in estimates of Pacific sardine biomass.

	Spawning biomass (tons)	Year	Citation	
Decline	3 000 000	1938	Murphy	1966
	300 000	1954	MacCall	1979
	30 000	1964	MacCall	1979
	?< 10 000	1972	Mais	1974
Recovery	30 000	1985	Barnes *et al.*	1992
	300 000	1995	Deriso *et al.*	1996

Pacific hake or whiting (*Merluccius productus*) because long time series of the reproductive environment of these species are available. Discussion of stock assessments will be minimized in this chapter owing to the comprehensive reviews in the context of CalCOFI stock assessment (Clark and Marr, 1955; Soutar and Isaacs, 1974; Lasker, 1985; Lo 1985,1986; Baumgartner *et al.*, 1992; Hunter and Lo, 1997; Lo 1997). Research needed for juvenile stages will be emphasized because of the failure of simple early larval abundance estimates of anchovy, sardine and hake to predict recruitment (Ahlstrom, 1965; Peterman *et al.*, 1988; Hollowed, 1992). Analysis of food demands of adults has not yielded information on population growth (Murphy, 1966; Riffenburgh, 1969; Lasker, 1970; Lasker 1985; Mullin and Conversi, 1988) but Ware and Thomson (1991) do associate recruitment success of sardine and hake in a half century time frame with upwelling, diatom abundance and plankton productivity.

It is the purpose of this chapter to focus on questions about the current state of fisheries oceanography, its potential for assisting managers to prevent recruitment overfishing (Myers, 1997), and to speculate on new mechanisms for CalCOFI and other research programme's to improve management of pelagic fisheries resources (Kendall and Duker, 1998). We will emphasize three major populations, anchovy, sardine, and hake. While one principal objective of CalCOFI has been to assemble a time series of population size, these assessment activities will not be covered in this chapter since fisheries oceanography is not directly involved in questions of biomass assessment.

2.2   How is the demographic strategy of anchovy, sardine and hake described?

These fish are characterized as having high and variable pre-recruit mortality rates, several over-lapping generations (5–15 years), with multiple-spawns per surviving female within and among seasons with spawns distributed widely in time and space. Murphy (1968) described the Pacific sardine as the virtual prototype of this style of life history. Later analyses and simulations (Hennemuth *et al.*, 1980; Spencer and Collie, 1997; Myers and Mertz, 1998; Gaggiotti and Vetter, 1999) have described time variation. These three species, anchovy, sardine and hake, with shared juvenile habitats, were placed in three different categories by Spencer and Collie (1997). Anchovy was determined to be 'irregular', sardine 'spasmodic' and hake 'steady-state'. Conditions under which such populations persist have been considered by Charlesworth (1994).

2.3   Why do fish populations vary?

Sissenwine (1984) states 'Recruitment is likely to be a multiplicative function of highly variable processes occurring throughout the first year of life, including the

post-larval stage.' Production and survival of embryos, survival and growth of larvae and juveniles and maturation are 'highly variable processes' (Cushing, 1985, 1988). Appreciation of the variability of processes led Gulland (1982) to ask 'Why do fish numbers not vary?' expressing wonder at how stable many species are, even under fishing pressure.

2.4   What are the objectives of the CalCOFI?

CalCOFI was founded in the mid-1940s to study the collapse of the Pacific sardine fishery but the objectives of the programme soon expanded based on the statement adopted in 1957 by John Radovich, John Isaacs, and John Marr:

'To determine what controls variation in population size and availability off the west coast of North America of sardines and, as their scientific and industrial importance requires, of anchovy, jack mackerel, Pacific mackerel, herring, squid, and others.'

These scientists represented three cooperating research groups: the California Department of Fish and Game (CDFG) marine division, the Marine Life Resources Group of the Scripps Institution of Oceanography of the University of California (SIO), and the Coastal Fisheries Research Division, La Jolla Laboratory of the National Oceanic and Atmospheric Administration, National Marine Fisheries Service.

In general the three agencies were charged with:

(1)   maintaining surveillance of the fisheries by standard monitoring and analysis of the catch and effort of the fishing fleets;
(2)   monitoring the chemical, physical and biological characteristics of the oceanic habitats of the pelagic species; and
(3)   monitoring the populations with fisheries independent techniques: in this case by ichthyoplankton sampling during physical oceanographic survey cruises (Marr 1960).

In addition to agency funded programmes, special research projects were funded by a self-imposed tax on the landings of the 'wetfish' species or more generally the purse-seine fleet. Reviews of CalCOFI fisheries oceanography after the first 10 years (Blackburn 1961) and 30 years of research were published by Hewitt (1988), Reid (1988) and Smith and Moser (1988). The accomplishments of CalCOFI have heretofore emphasized assessment and environmental description: this review will attempt to highlight the need for an increased emphasis on recruitment prediction and the enhanced environmental analysis that will be required.

2.5   Why do density-dependent controls on pelagic recruitment appear so weak?

The principal effects of density-dependence are subtle factors which slowly regulate reproductive success in numerous heterogeneous pelagic habitats. Local species crowding may merely result in regional offshore migrations leading to only subtle changes in growth and mortality (MacCall, 1990). For juveniles invading adult habitats high risks of juvenile mortality are imposed by the behaviour of breaking schools to feed (Nonacs *et al.*, 1994; Nonacs *et al.*, 1998). After maturation, limited food may simultaneously make first spawners small, and make repetitive spawners limit the eggs per batch or number of batches per year. In these trophic interactions, habitat productivity may be low or the local population may be densely distributed. Studies conducted on this situation will remain ambiguous until the research elucidates the controlling processes (Mullin, 1993; Shenk *et al.*, 1998).

Bailey *et al.* (1996) have enunciated a more thorough process for examining field data on recruitment in pelagic fisheries called 'multiple life stage control'. That is, the life stage of origin of recruitment failure ('critical period') can arise at any pre-recruitment stage. Strong (1986) has referred to density 'vague' population growth rate controls which work only at the extremes of population density. Only a small fraction of the spawning adults contribute to the recruit population in the 'Hedgecock hypothesis' (Hedgecock 1994a; 1994b): Gaggiotti and Vetter (1999) have simulated the genetic consequences of recruitment variation in populations with high fecundity and low survival rates to recruitment. Even though density-dependence is considered weak in these populations for interannual controls on population growth, it must play a major and consistent role as the upper limits of population size and density are approached.

2.6   What is the critical scale of the habitat?

The anchovy is best understood in this regard. This species' spawning biomass in the California Current area was about a million tons in the early 1970s (Jacobson *et al.*, 1994). Two structures are thought to be important: schools and school groups (Smith *et al.*, 1989). For the purpose of this argument, the radius of a school is 20 m and the radius of a school group 20 km. At $4 \, \mathrm{kg \, m^{-2}}$, the schools of this population covered a quarter billion square metres. At $1200 \, \mathrm{m^2} \, \mathrm{school^{-1}}$ this would be about 200 000 schools. If $\frac{1}{5}$ of the females in each school spawned each night, there would be 1 million egg habitats in a heterogeneous sea for each batch of eggs. If the mature females spawned 20–30 batches per year, one could refer to the launching of 25 million egg habitats spread through the spawning season. These habitats, at this scale, are somewhat independent of each other and the survival rates of embryos, no matter how variable, would, in the aggregate, result in a production of larvae which was relatively invariant.

By the virtual disappearance of some embryo patches by advection, thinning of patches by predation, and the fusion of the original embryonic habitats caused by the lengthening radius of influence of juveniles, we would expect there to be 10s to 100s of school groups for the juveniles to invade at recruitment. Thus from millions of heterogeneous habitats for eggs at the centimetre scale, we have generated a relatively small number of schools of juveniles which must successfully invade *c*. 100 school groups. In a half year, the critical scale for population reproductive success changes from micrometres for fertilization, to centimetres for first feeding, to kilometres for juveniles with concomitant changes in the size and number of habitat units. In this way, the unit variability of the embryonic stage (Bradford, 1992) could be higher than the variability of the juvenile stage, but the number of juvenile spatial units has been reduced so drastically that the resultant recruitment variability is in effect, higher than that of any earlier stage (Smith, 1978; Smith and Moser, 1988).

2.7   How can recruitment models of anchovy, sardine and hake populations be initiated?

A first step is to gather information on parameters from population assessments and assemble them into a plausible deterministic skeleton matrix (Leslie, 1945; Lefkovitch, 1965; Paulik, 1973; Caswell, 1989; Higgins *et al.*, 1997). Even though the assumed population equilibrium and stationarity is implausible for projecting population size, simple models can be useful at the conceptual level. The mathematical scope of life-stage parameters has been postulated for three California Current representatives of the genera; anchovy, sardine, and hake (Lo *et al.*, 1995; Butler *et al.*, 1993; Smith *et al.*, 1992; Smith, 1995). The values for four stages, embryonic, larval, juvenile, and adult, for each of the three species is given in Table 2.2. This is an artificial assembly of plausible values for growth and mortality scaled to the oldest female survivor of the cohort in all three species. A survivor of the juvenile stage will have increased its individual weight by many fold in each species with the required food consumption a small multiple of that. Furthermore, variations in the production of adults (Table 2.2) identify a further need for food production estimates for the occasional extreme years of high recruitment on a generation to decadal time scale.

2.8   What does a recruitment time series look like?

Figure 2.1 illustrates the recruitment characteristics of anchovy, sardine and hake. The time series of relative recruitment rates (left column) is indicative of the population's own control of the increase of the population. The range of ratios is high for all three species. The time series of the *absolute* recruitment rates (right

Table 2.2   Life table for anchovy, sardine and hake

Stage	Age (yr)	Age (days)	Anchovy Number (n)	Beginning Live weight (g)	Beginning Biomass (g)
Embryo*	0	1	34 350 096	0.00036	1.24E+04
Larvae	0.018	7	3 593 062	0.00009	3.23E+02
Juveniles	0.18	62	5 022	0.019	9.54E+01
Adults	0.56	205	265	5	1.33E+03
	7.5	2743	1	24.5	2.45E+01
Postulated Recruitment Range	48>265>1451				

Stage	Age (yr)	Age (days)	Sardine Number (n)	Beginning Live weight (g)	Beginning Biomass (g)
Embryo*	0	1	73 684 823	0.0026	1.92E+05
Larvae	0.019	7	5 411 882	0.00064	3.46E+03
Juveniles	0.15	55	28 260	0.021	5.93E+02
Adults	1.26	460	82	25	2.05E+03
	12.2	4471	1	205	2.05E+02
Postulated Recruitment Range	11>82>635				

Stage	Age (yr)	Age (days)	Hake Number (n)	Beginning Live weight (g)	Beginning Biomass (g)
Embryo*	0	1	7 798 921	0.000746	5.82E+03
Larvae	0.04	16	833 589	0.000566	4.72E+02
Juveniles	0.32	117	448	0.113	5.06E+01
Adults	1.97	720	37	336	1.24E+04
	20	7287	1	1300	1.30E+03
Postulated Recruitment Range	3.7>37>370				

* egg and yolk-sac larvae

column) is indicative of the capacity of the environment to allow an increase in the populations. If the carrying capacity was to be reached, the *absolute* recruitment rate would exhibit a maximum in a long time series. There are not sufficient overlaps in these series to show interactions, if any. Serial autocorrelation has been noted for the sardine (Murphy, 1966). The anchovy appears to be somewhat less autocorrelated. First level predictions for these species could be based on continuity; i.e. the recruitment next year is expected to be a repeat of this year. Conversely, for hake there appears to be negative autocorrelation (possibly due to
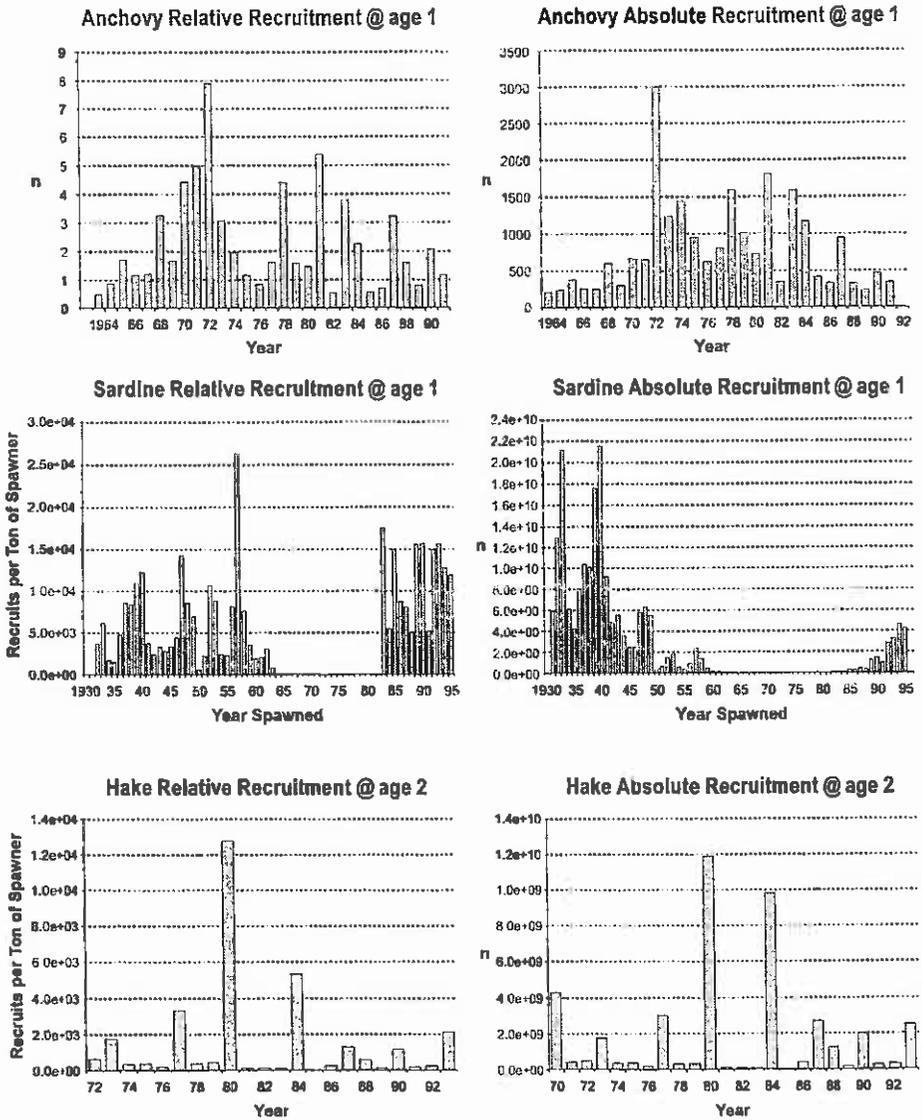
Fig. 2.1 Recruitment in three major stocks which reproduce in the California Current Region: anchovy (Jacobson *et al.*, 1994), sardine (Barnes *et al.*, 1997; Jacobson and MacCall, 1995) and hake (Dorn, 1996). In the left column of figures are the relative rates of recruitment success expressed in units of recruitment per unit of spawner (ton (t) per t of spawning biomass, anchovy; individuals per t of spawning biomass, sardine and hake). In the right column are the absolute rates of recruitment success (t, anchovy; individuals, sardine and hake).

late juvenile cannibalism on early juveniles) and a first level prediction could be that recruitment next year will be low if this year's recruitment is high.

2.9   What is the frequency distribution of reproductive success?

In the California Current anchovy, sardine and hake (Fig. 2.2) there is a marked deficiency of values in the area of 1, 'equilibrium'. If we assume an average value of one for the millennia that these species have occupied this habitat, the distribution of extreme values of recruitment per unit population is the rule with a mixture of extreme and moderate recruitment 'failures' sustained by relatively infrequent and extreme recruitment success. The geographic extent of the sardine and hake habitats are similar with the exception that the hake lives between 50 and 500 m (Wilson *et al.*, 1997) while the sardine lives mostly in the upper 50 m. This may mean that the difference in the success of recruitment is related to local phenomena in the vertical plane, rather than regional, basin or global scale phenomena. This poses problems for the systematic study of recruitment since the processes controlling population size, span a long series of recruitment failure interrupted by short episodes of recruitment success. It should be pointed out that the scale deposition records for anchovy, sardine and hake assembled in 5-year intervals do show a central tendency (Smith, 1978) in relative reproductive success. Sardine variation at this scale is higher because of interannual coherence among successive recruitments (Murphy, 1966) seen in contemporary sardine populations. The absence of central tendency in annual recruitment success and its presence of a central tendency in the decadal scale suggests that population controls, either demographic or environmental, operate at or near generation or decadal scales.

2.10   What are the major questions for CalCOFI research?

There are at least four major questions to pursue to contribute to better understanding of the interaction of schooling coastal pelagic fish populations and the California Current region environment.

(1) Why is variability of recruitment among years higher than the variability of any of the preceding planktonic stages?

(2) Why are annual recruitment rates which would lead to equilibrium population size only rarely observed for all three species?

(3) Why does recruitment of the shorter lived anchovy vary less than the recruitment of sardines and hake?

(4) Why do warm, plankton poor years favour recruitment of anchovy, sardine (Sette, 1959) and hake (Swartzman *et al.*, 1983)?
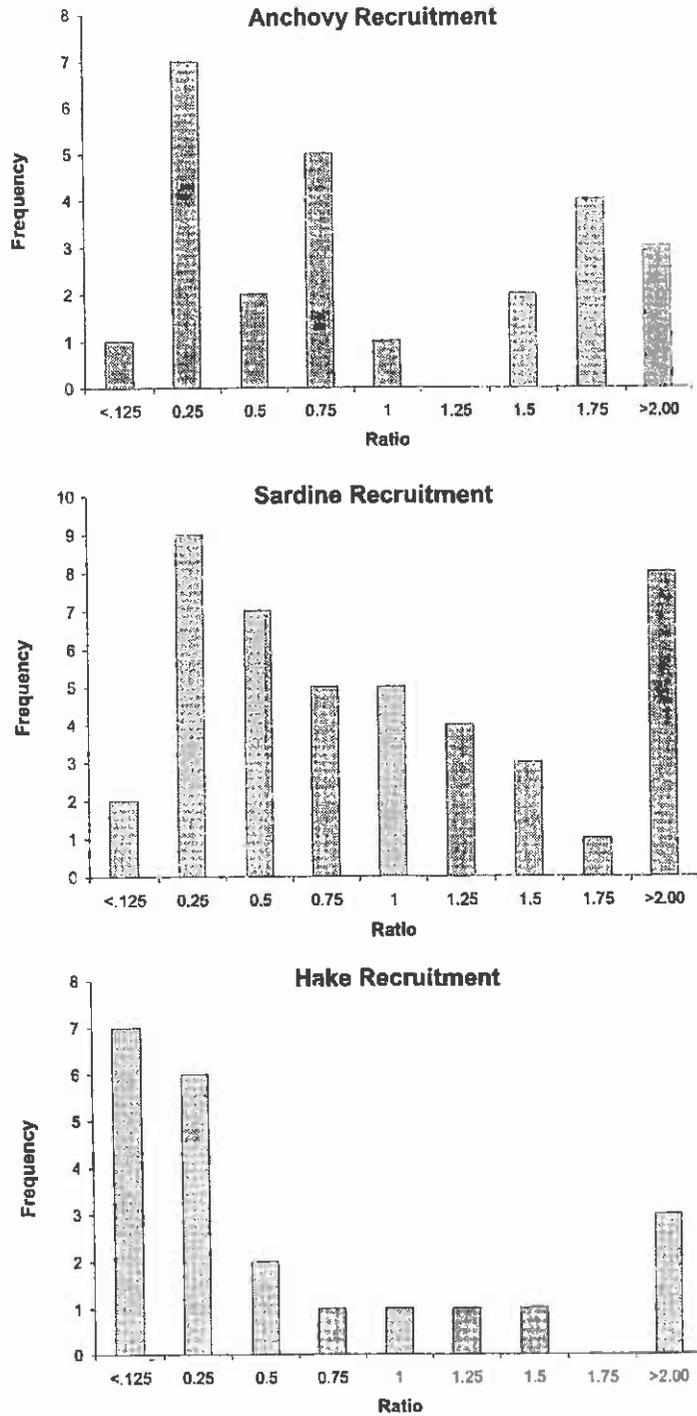
Fig. 2.2 Grouped recruitment frequency normalized to a unit (arithmetic mean) recruitment success. Annual average recruitment would exhibit a mode at 1 with varying degrees of deviation to the fractions and multiples on the abscissa.

It has been noted for anchovy (Smith and Moser, 1988), sardine (Smith, 1978) and hake (Hollowed, 1992) that the variability of recruitment is much higher than the variability of any of the planktonic stages. This means that the absolute variability plus the error of estimation increases as the juvenile fish approach recruitment. If the spatial relations of hake and sardine resemble the anchovy (above) they may also be explained by the launch of a multitude of embryo cohorts resulting in the recruitment of a small number of juvenile aggregations.

Concomitant with the above observation on recruitment variability, Fig. 2.2 shows that an 'average' recruitment is a rarity. The modal recruitment in all three stocks is well below average and the usual observation of the conditions around recruitment will be a recruitment failure, broken occasionally with a large reproductive success.

The sardine and hake populations are distributed along the entire west coast of North America and are long-lived relative to anchovy. The longer life cycles probably allow tolerance of greater interannual variability in recruitment than observed in the anchovy. Recently observed recruitment to the anchovy stock has varied 30-fold, sardine recruitment has varied 60-fold, and hake recruitment has varied 100-fold. In contrast, local Dover Sole (*Microstomus pacificus*) recruitment varied less than 10-fold (Brodziak *et al.*, 1997) Recruitment of these species, as inferred from scale deposition rate in varved sediments, has varied in the same order over the last two centuries (Smith, 1978). This is counter to the theoretical expectation that populations with shorter life spans, and therefore fewer cohorts extant, are more variable.

It is generally perceived that the California Current system is enriched by two sources: equatorward transport of richer North Pacific waters and offshore transport of coastal surface waters which are then replaced by nutrient-rich upwelled waters. A major consequence of this is that years with colder surface layers are associated with years of higher zooplankton displacement volume (Reid *et al.*, 1958; Reid, 1962; Roemmich and McGowan, 1995a). Why should three major populations of fishes, all planktivorous in the pre-recruit stages, have higher recruitment in warm rather than in cold years?

2.11 How do we proceed with population level work given these questions?

It is always dangerous to predict what will not work. There is a chance that individually based models will lead to defining insight as in Hermann *et al.* (1996). At the other extreme, ecosystem-level trophic-cascade models could clarify the major questions of recruitment change and environmental controls on population growth (Jarre-Teichmann and Christensen, 1998). My insight leads me to believe that a factor analysis of contemporary cohorts of anchovy, sardine and hake is more likely to contribute in the short term as in Bailey *et al.* (1996). This is practical, since a fishery independent survey can give spawning biomass and monitoring of the fish-

eries can give an estimate of recruitment. This leaves only an estimate of juvenile abundance and growth to establish where recruitment is determined in the life history. Probably the first series of questions for these three species will relate to the consistency – how often is recruitment controlled by production of embryos? – survival of first feeding larvae? – growth and survival of late larvae and juveniles? If the answers consistently identify a stage transition as 'critical', the research can focus on that stage and its environment. A worst case scenario is that the determining events for all three species are independent and are spread among all of the transitions: in this case all factors will have to be monitored for predictions of recruitment.

2.12   What does the 'average' recruitment mean for fisheries management?

Figure 2.2 shows clearly that when contemporary allowable catch is estimated future recruitment should be discounted from the 'average' to the 'modal' recruitment. In anchovy and sardine less than 25% of the required replacement occurs most commonly. For hake, allocation of the next year's catch should not include projections of recruitment above 8%. In fact, it could be assumed that recruitment will fail for the purpose of setting the allowable catch of hake. When the occasional large recruitment occurs there is a decade when that catch rate can be augmented. (See meta-analysis by Myers and Mertz, 1998; also see Richards and Maguire, 1998, for a precautionary approach).

2.13   How does fisheries oceanography research contribute to improved management of fisheries?

The emphasis in fisheries management will eventually proceed from stock to species management and further to management of biological communities and large marine ecosystems. This will require an increase in the intensity of sampling to explore the population at the level where processes are controlling population growth and compensation for fishing pressure (Gulland, 1988). It will also require aggregation of research efforts into regional and basin studies to detect and accommodate climatic regime shifts. Large predator populations also migrate at basin scale and must be considered in fisheries impacts at the ecosystem level. General properties of oceanic habitat, such as productivity and inter-habitat transport will have to be described and monitored for ecosystem-level fisheries management.

2.14 Conclusions

(1) Contrary to expectations, variability of recruitment among years is higher than the interannual variability of the abundance of preceding planktonic stages. Contrary to expectations, annual recruitment rates which would lead to equilibrium population size are only rarely observed for all three species. Contrary to expectations, recruitment of the shorter lived anchovy varies less than the recruitment of sardines and hake. Contrary to expectations, warm, plankton poor years favour recruitment of anchovy, sardine and hake.

(2) The high variability of reproductive success is likely to be caused by strong controls of the environment on the survival and growth of the juvenile populations as they prepare to invade adult habitats.

(3) The inter-annual regularity of production of embryonic and larval stages is based on many, essentially independent habitats spread through time and space in the basic risk-spreading reproductive behaviour of the adults of anchovy, sardine and hake.

(4) Anchovy, sardine and hake habitats differ in the degree of dependence on offshore and nearshore habitats – the hake being more dependent on the hydrographic offshore features, the sardine occurring in both hydrographic and topographic habitats, and the anchovy occurring mostly in the topographic features. If we consider the offshore 'hydrographic' features to be the most variable, this could explain why the recruitment of hake is more variable than that of the sardine and anchovy.

(5) Warm periods may be characterized as spring-summer persistence of anticyclonic gyres which provide multiple hydrographic habitats while colder periods may force sites of reproducing success closer to the more highly populated topographic habitats and more predatory fauna.

2.15 Future directions

To face the challenges of future natural and social disarray resulting from harvesting marine fish species at the crest of their production, we must broaden the study of marine biological production. The grand structural concepts of 'ecosystem approach', 'large marine ecosystems', 'marine reserves' will need to be constructed for field tests, interpreted at several scales, and enabled by appropriate monitoring. The existing network of catch monitoring, sustainable harvest modelling, and fisheries independent assessment at the population level must not be abandoned in the quest for new broad-based management. The time series of multi-decadal length, at the population scale, will be our only quality control tool for several decades of newer comprehensive procedures. In this section, I will briefly outline procedures which now seem possible at scales larger and smaller than current management attention.

Large scale procedures

It is time to re-assemble basin (North Pacific) and regional (NE Pacific) meta-analyses (Baumann and LeBlond, 1996) to expand on the approach of Hollowed *et al.* (1987). One tactic is to contrast successful and failing reproductive seasons with ensembles from meteorological and oceanographic data. We have had 50 years of CalCOFI, and decadal research of Global Climate Modeling (GCM), the World Ocean Circulation Experiment (WOCE), Joint Global Ocean Fluxes Study (JGOFS), Global Ocean Ecosystems Dynamics (GLOBEC), North Pacific Marine Science Organization (PICES), and Fisheries Oceanography Coordinated Investigations (FOCI), and planning level Ocean Ecology: Understanding and Vision for Research, and foundation work on large marine ecosystems based on ECOPATH and ECOSIM (Jarre-Teichmann and Christensen, 1998).

Small scale procedures

While much biological information has been assembled from CalCOFI field surveys, laboratory studies, and modelling, there has not been sufficient response of time-series field work to this information. Items which require additional small-scale work are:

(1) microbial loop dynamics over large areas (Ohman *et al.*, 1991);

(2) work on structured and unstructured trophic food webs supporting major fish, copepod and euphausiid populations (Isaacs, 1973; Colebrook, 1976; Childress *et al.*, 1980);

(3) school and school group regional growth studies in support of Individual Based Models of pelagic fishes (Brandt and Kirsch, 1993; Brodeur *et al.*, 1996; Swartzman *et al.* 1999; Diachok, 1999);

(4) detailed physical and biological analyses of the formation, structure and persistence of large anticyclonic eddies (Owen, 1980, 1981; Lynn and Simpson 1987; Moisan and Hofmann, 1996a, 1996b, 1996c; and Pares-Sierra *et al.*, 1993);

(5) revision of definitions of domain boundaries and population exchange rates among habitats using genetic evidence (Ware and McFarlane, 1989; Hedgecock *et al.*, 1989; Rocha-Olivares and Vetter, 1999; Gaggiotti and Vetter, 1999);

(6) interdecadal (10–20 years) surveys at the basin or regional scale to evaluate contrasting conditions at the scale of regime shifts.

There are some indications that large coastal anticyclonic eddies deserve special attention in the California Current region. For example, Roessler and Chelton (1987) found that there are transient (on the time scale of months) offshore rich

habitats derived from coastal filaments. They detected six episodes in their three decade record, the most recent of which was 1980. Some coastal filaments may become entrained to the periphery of offshore and long-lived anticyclonic eddies (Bakun, 1997). (For contrast see the exit times analysis for cyclonic eddies on the time scale of weeks by Denman *et al.*, 1989.)

The Roessler/Chelton mechanism for generating static offshore mesoscale habitats may provide temporary offshore brood habitats for nominally coastal species. Pelaez and McGowan (1986) illustrate the structure of the eddies in a description of the pigment patterns. It is clear from their illustrations that small peripheral margins contain most of the chlorophyll and the warm core occupies most of an anticyclonic eddy. While the large warm core increases the large-scale average temperature, the productive periphery could be the site of additional offshore brood zones. On the occasions when this happens one may expect coastal larvae and juveniles to be inserted into a transient coast-like habitat which could foster rapid growth away from the predatory coastal nekton, birds and mammals.
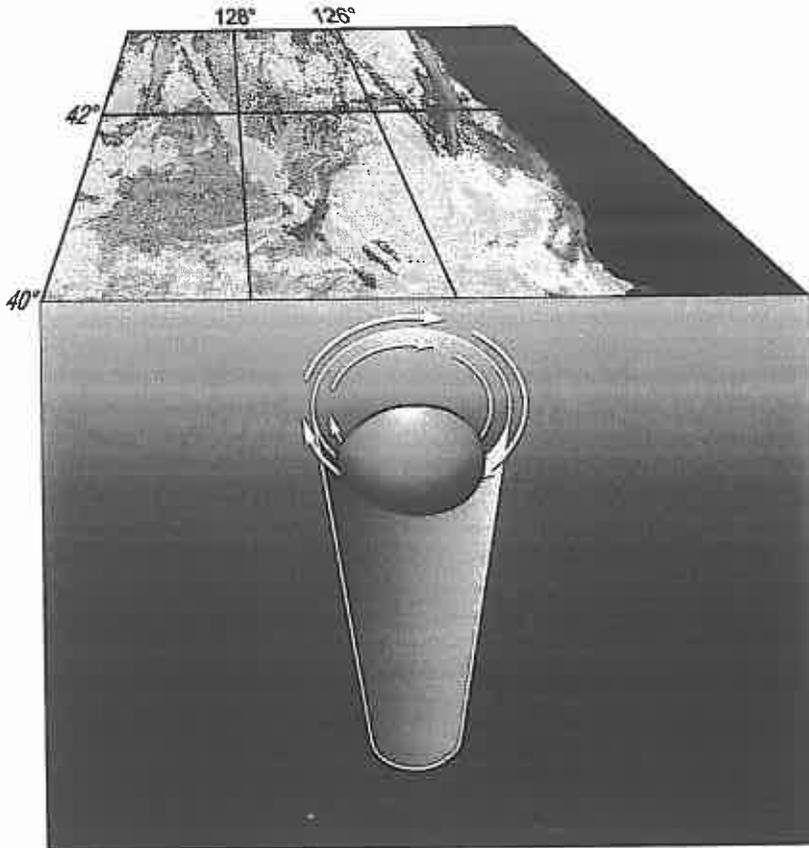

Fig. 2.3 Suggested mechanism for production and succession within an anticyclonic eddy. Sea-WiFS 1998 March 17, 21:28:40 GMT. Diagram appended by Henry Orr. Red tones of chlorophyll exceed $5 \, \text{mg m}^{-3}$.

A dipole eddy could couple offshore regions of high larval growth rate (Owen, 1980) and survival in the cyclonic eddy with subsequent injection of the larvae from the periphery of the cyclonic to the rich periphery (Haury, 1984) of the anticyclonic eddy. Here the range of habitats could match the changing food demands of the rapidly growing larvae. The Margalef 'mandala' (his figure 2 1978; also see Estrada and Berdalet 1997) offers an intricate structure which would characterize the periphery of an anticyclonic eddy (Fig. 2.3). Distal to the axis in the shear zone would be diatom and copepod growth and closer to the centre would be more stable regions fostering dinoflagellate growth; if such a structure were to persist for the months necessary for the juvenile period of fishes, then such a structure or series of structures (Fig. 2.4) could contribute materially to the production of recruitment of fishes.
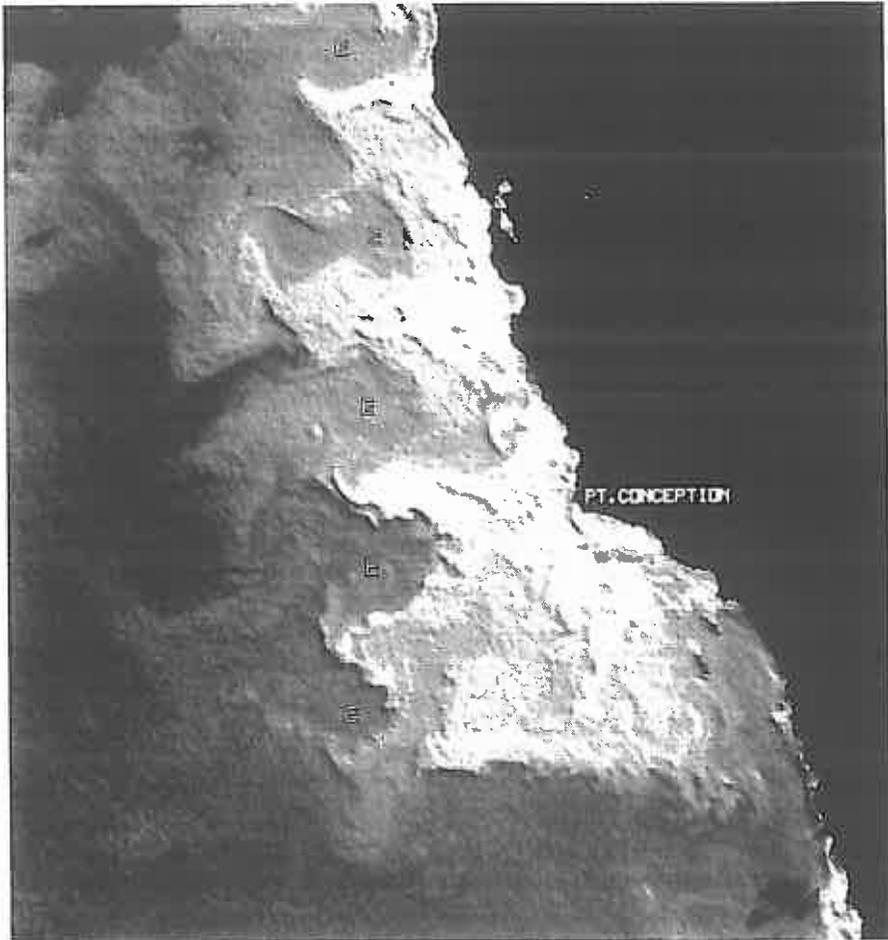

Fig. 2.4 An example of multiple mesoscale eddies (five eddies denoted as E in chlorophyll gradient enhanced Satellite Coastal Zone Color Scanner June 15, 1981) along the California Current region (Fiedler, 1984).

Since the production of nauplii may be at some depth (Mullin and Cass-Calay, 1997), satellite images need accompanying measurement and analysis of the vertical structure of the warm core eddies. The succession of organisms in time and their distribution in space would offer an ideal habitat for the changing requirements for feeding from larval to late juvenile stages in close proximity. It is possible for some expatriates from coastal spawning areas and nursery habitats to thrive in an offshore productive brood habitat (Arthur, 1977). The additional area of brood habitat may then be the source of variability of recruitment. When the California Current area is occupied by anticyclonic eddies or warm core rings, all but the periphery would be warm and unproductive (McGillicuddy and Robinson, 1997). The peripheral brood zones would be an important addition to the limited coastal brood habitats. In this way, the variability of recruitment of anchovy is less than that of hake or sardine because of the more nearshore habitat of the anchovy. Episodes of anticyclonic eddy-dominated recruitment would occur least in anchovy, secondarily in sardine and principally in hake because of the proximity to the coastal slope.

Owen (1980) and Burkov and Pavlova (1980) have provided extremely useful statistical summaries of eddies by season, region and size in the California Current system. This work is being followed up by a time-series and climatology of eddy formation, location and persistence (Logerwell pers. comm). If there is a link to larger-scale dynamics of subarctic and tropical systems in terms of formation and persistence of anticyclonic eddies this link could be used for predictions in the future and interpretation of older meteorological and tidal height records as in Pares-Sierra *et al.* (1993).

Note

Time series data used in this chapter can be found at *http://swfsc.ucsd.edu/paulsmith/*

Acknowledgments

Literature Cited

Ahlstrom, E. H. 1965. A review of the effects of the environment on the Pacific sardine. International Commission of the
Northwest Atlantic Fisheries Special Publication No. 6:53

Arthur, D. K. 1977. Distribution, size and abundance of microcopepods in the California Current System and their possible
influence on survival of marine teleost larvae. Fish. Bull. U. S. 75:601-611

Bailey, K. M., R. D. Brodeur, and A. B. Hollowed. 1996. Cohort survival patterns of walleye pollock, Theragra
chalcogramma, in Shelikoff Strait, Alaska: a critical factor analysis. Fisheries Oceanography 5 (Suppl. 1):179-188

Bakun, A. 1997. Radical interdecadal stock variability and the triad concept: A window of opportunity for fishery management
science, pp. 1-18 [in] Pitcher, T. J., P. J. B. Hart and D. Pauly, eds. Reinventing Fisheries Management. Chapman and Hall,
London

Barnes, J. T. , L. D. Jacobson, A. D. MacCall, and P. Wolf. 1992. Recent population trends and abundance estimates for the
Pacific sardine (Sardinops sagax). California Cooperative Oceanic Fisheries Investigations Reports 33:60-75

Baumann, M. and P. H. LeBlond. 1996. Climate change and fish production in the northeast Pacific: the missing links. World
Resource Review 8:2:139-157

Baumgartner, T. R., A. Soutar, and V. Ferreira-Bartrina. 1992. Reconstruction of the history of Pacific sardine and northern
anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. California Cooperative
Oceanic Fisheries Investigations Report 33:24-40.

Bradford, M. J. 1992. Precision of recruitment predictions from early life stages of marine fishes. Fishery Bulletin, U. S.
90:439-453

Brandt, S. B. and J. Kirsch. 1993. Spatially explicit models of striped bass growth potential in Chesapeake Bay. Transactions
of the American Fisheries Society 122:845-669.

Brodeur, R. D., J. M. Napp, M. T. Wilson, S. J. Bograd, E. D. Cokelet, and J. D. Schumacher. 1996. Acoustic detection of
mesoscale biophysical features in the Shelikof sea valley, and their relevance to pollock larva in the Gulf of Alaska. Fisheries
Oceanography 5 (Suppl. 1):71-80

Brodziak, J., L. Jacobson, R. Lauth, and M. Wilkins. Assessment of the Dover Sole Stock for 1997. In Pacific Fishery
Management Council. 1997. Appendix: Status of the Pacific Coast Groundfish Fishery Through 1997 and Recommended
Biological Catches for 1998: Stock Assessment and Fishery Evaluation. Pacific Fishery Management Council, 2130 SW Fifth
Avenue, Suite 224, Portland, Oregon 97201

Blackburn, M. 1961. Symposium on fisheries oceanography. CalCOFI Rep. 8:21

Burkov, V. A. and Y. V. Pavlova. 1980. Description of the eddy field of the California Current. Oceanology 20:272-

Butler, J. L., Smith, P. E. and N. C. H. Lo. 1993. The effect of natural variability of life-history parameters on anchovy and
sardine populations. CalCOFI Reports 34:104-111

Caswell, H. 1989. Matrix population models. Sinauer Associates Inc Sunderland Massachusetts

Charlesworth, B. 1994. Evolution in age-structured populations. 2nd Edition. Cambridge University Press Cambridge UK
306p

Childress J. J.. S. M. Taylor, G. M. Cailliet, and M. H. Price. 1980. Patterns of growth, energy utilization and reproduction in
some meso- and bathypelagic fishes off Southern California. Marine Biology 61: 27-40.

Clark, F. N. and J. C. Marr. 1955. Population dynamics of the Pacific sardine. CalCOFI Rep. 4:11-48

Colebrook, J. M. 1976. Annual fluctuations in biomass of taxonomic groups of zooplankton in the California current, 1955-59.
Fishery Bulletin U. S. 75:357-368

Cushing, D. H. 1985. Reporter's Summary. Canadian Journal of Fisheries and Aquatic Sciences 42:275-278

Cushing, D. H. 1988. The study of stock and recruitment. Pp105-128 In "Fish Population Dynamics" , J. A. Gulland, ed.
Wiley Chichester

Denman, K. L., H. J. Freeland, and D. L. Mackas. 1989. Comparisons of time scales for biomass transfer up the marine food
web and coastal transport processes. Pp255-264 In Beamish, R. J. and G. A. McFarlane [eds] Effects of ocean variability on
recruitment and an evaluation of parameters used in stock assessment models. Can. Spec. Publ. Fish. Aquat. Sci. 108

Deriso, R. B., J. T. Barnes, L. D. Jacobson, and P. R. Arenas. Catch-at-age analysis for Pacific sardine (Sardinops sagax),
1983-1995. California Cooperative Oceanic Fisheries Investigations Reports 37:175-187

Diachok, O. 1999. Effects of absorptivity due to fish on transmission loss in shallow water. J. Acoustical Society of America
105:2107-2129

Dorn, M. W. 1996. Status of the Coastal Pacific Whiting Resource in 1996. Appendix A Alaska Fisheries Science Center,
National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, BIN 15700
Seattle, WA 98115-0070

Estrada, M. and E. Berdalet. 1997. Phytoplankton in a turbulent world. Scientia Marina 61:Suppl. 1:125-140

Fiedler, P. C. 1986. Offshore entrainment of anchovy spawning habitat, eggs, larvae by a displaced eddy in 1985. CalCOFI
Rep. 27:144-152

Gaggiotti, O. E. and R. D. Vetter. 1999. Effect of life-history strategy, environmental variability, and overexploitation on the
genetic diversity of pelagic fish populations. Canadian Journal of Fisheries and Aquatic Sciences 56:1376-1388

Gulland, J. A. 1982. Why do fish numbers vary? Journal of Theoretical Biology 97:69-75

Gulland, J. A. 1988. The problems of population dynamics. P 383-406 in "Fish Population Dynamics (Second Edition) J. A.
Gulland [ed] Wiley and Sons Ltd New York

Haury, L. R. 1984. Plankton Distributions. Pp 95-111 in An offshore eddy in the California Current System, Simpson, J. J., C.
J. Koblinsky, L. R. Haury, and T. D. Dickey (eds.) Progress in Oceanography 13:1:1-111

Hedgecock, D. 1994a. Temporal and spatial genetic structure of marine animal populations in the California Current. CalCOFI
Rep. 35:73-81

Hedgecock, D. 1994b. Does variance in reproductive success limit effective population sizes of marine organisms? Chapter 2.5
pp 122-134 In 'Genetics and evolution of aquatic organisms' A. R. Beaumont (ed.) London; New York: Chapman and Hall

Hedgecock, D., E. S. Hutchinson, G. Li, F. L. Sly, and K. Nelson. 1989. Genetic and morphometric variation in the Pacific
sardine, Sardinops sagax caerulea: comparisons and contrasts with historical data and with variability in the northern anchovy,
Engraulis mordax. Fish. Bull. U. S. 87:653-671

Hennemuth, R. C., J. E. Palmer, and B. E. Brown. 1980. A statistical description of recruitment in eighteen selected fish
stocks. J. Northw. Atl. Fish. Sci. 1:101-111

Hermann, A. J., S. Hinckley, B. A. Megrey, and P. J. Stabeno. 1996. Interannual variability of the early life history of walleye
pollock near Shelikof Strait as inferred from a spatially explicit, individual-based model. Fish. Oceanogr. 5(Suppl.1) 39-57

Hewitt, R. P. 1988. Historical review of the oceanographic approach to fishery research. CalCOFI
Rep. 29:27-41

Higgins, K, A. Hastings; J. N. Sarvela, and L. W. Botsford. 1997. Stochastic dynamics and deterministic skeletons: Population
behavior of Dungeness crab. Science 276(5317):1431-1435.

Hollowed, A. B. 1992. Spatial and temporal distributions of Pacific hake, Merluccius productus, larvae and estimates of
survival during early life stages. CalCOFI Rep 33:100-1123

Hollowed, A. B., K. M. Bailey, and W. S. Wooster. 1987. Patterns in recruitment of marine fishes in the northeast Pacific

Ocean. Biol. Oceanog. 5:99-131.

Hunter, J. R. and N.C.H. Lo. 1997. The daily egg production method of biomass estimation: some problems and potential
improvements. Ozeanografika 2:41-69

Isaacs, J. D. 1973. Potential trophic biomasses and trace-substance concentrations in unstructured marine food webs. Mar.
Biol. 22:97-104

Jacobson, L. D., N. C. H. Lo, and J. T. Barnes. 1994. A biomass-based assessment model for northern anchovy, Engraulis
mordax. Fishery Bulletin 92:711-724

Jacobson, L. D. and A. D. MacCall. 1995. Stock-recruitment models for Pacific sardine (Sardinops sagax). Can. J. Fish.
Aquat. Sci 52:566-577

Jarre-Teichmann, A. and V. Christensen. 1998. Comparative modeling of trophic flows in four large upwelling ecosystems:
global vs. local effects. p. 423-443. In Durand, M.-H., P. Cury, R. Mendelssohn, C. Roy, A. Bakun, and D. Pauly (eds.)
Global vs. Local Changes in Upwelling Ecosystems. Orstom, Série Colloques et Seminaires, Paris.

Kendall, A. W. and G. J. Duker. 1998. The development of recruitment fisheries oceanography in the United States. Fisheries
Oceanography 7:2,69-88

Lasker, R. 1970. Utilization of zooplankton energy by a Pacific sardine population in the California Current, p. 265-284. In J.
H. Steele (ed.), Marine Food Chains. Univ. Calif. Press, Berkeley

Lasker, R. 1975. Field criteria for survival of larval anchovy: the relation between inshore chlorophyll maximum layers and
successful first feeding. Fish. Bull. U. S. 73:453-462

Lasker, R. 1985. What limits clupeoid production? Can. J. Fish. Aquat. Sci. (Suppl. 1):31-38

Lasker, R. ed. 1985. An egg production method for estimating spawning biomass of pelagic fish: application to the northern
anchovy, Engraulis mordax. NOAA Tech. Rep. NMFS 36. 99 pp.

Lasker, R. and A. MacCall. 1983. New ideas on the fluctuations of the clupeoid stocks off California. Pp 110-120 [In]
Proceedings of the Joint Oceanographic Assembly 1982, General Symposia, Dalhousie Univ. Halifax, Nova Scotia, Canada

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics 21:1-18

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183-212

Lo, N. C. H., P. E. Smith, and J. L. Butler. 1995. Population growth of northern anchovy and Pacific sardine using
stage-specific matrix models. Mar. Ecol. Prog. Ser. 127:15-26

Lynn, R. J., and J. J. Simpson. 1987. The California Current system: the seasonal variability of its physical characteristics. J.
Geophys. Res., 92:12947-12966

MacCall, A. D. 1979. Population estimates for the waning years of the Pacific sardine fishery. California Cooperative Oceanic
Fisheries Investigations. Rep. 20:72-82

MacCall, A. D. 1990. Dynamic geography of marine fish populations. University of Washington Press Seattle 153 p

Mais, K. F. 1974. Pelagic fish surveys in the California Current. California Department of Fish and Game, Fish Bulletin 162, 79
pp.

Margalef, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanologica Acta
1:493-509

Marr, J. C. 1960. The causes of major variations in the catch of the Pacific sardine Sardinops caerulea (Girard). Pp 667-791
in Proceedings of the World Scientific Meeting on the Biology of sardines and related species Volume 3. H. Rosa, Jr. and G.
Murphy [eds] Rome, FAO

McGillicuddy, D. J. Jr., and A. R. Robinson. 1997. Eddy-induced nutrient supply and new production in the Sargasso Sea.
Deep-Sea Research I, 44:1427-1450

Moisan, J. R. and E. E. Hofmann. 1996a. Modeling nutrient and plankton processes in the California coastal transition zone: 1.)
A time- and depth-dependent model. Journal of Geophysical Research 101:C10:22647-22676.

Moisan, J. R. and E. E. Hofmann. 1996b. Modeling nutrient and plankton processes in the California coastal transition zone:
2.) A three-dimensional physical-bio-optical model. Journal of Geophysical Research 101:C10:22677-22691.

Moisan, J. R. and E. E. Hofmann. 1996c. Modeling nutrient and plankton processes in the California coastal transition zone: 3.)
Lagrangian drifters. Journal of Geophysical Research 101:C10:22693-22704.

Mullin, M. M. 1993. Webs and scales: physical and ecological processes in marine fish recruitment. Washington Sea Grant
Program, Seattle 135 p

Mullin, M. M. and S. L. Cass-Calay. 1997. Vertical distributions of zooplankton and larvae of the Pacific hake (Whiting),
Merluccius productus, in the California Current system. CalCOFI Rep 38:127-136

Mullin, M. M. and A. Conversi. 1988. Biomasses of euphausiids and smaller zooplankton in the California
Current--Geographic and interannual comparisons relative to the Pacific whiting, Merluccius productus, fishery. Fishery
Bulletin, U. S. 87:633-644

Murphy, G. I. 1966. Population biology of the Pacific sardine (Sardinops caerulea). Proc. Calif. Acad. Sci. 34:1-84.

Murphy, G. I. 1968. Pattern in life history and the environment. American Naturalist 102:391-403

Myers. R. A. 1997. Comment and reanalysis: paradigms for recruitment studies. Can. J. Fish. Aquat. Sci. 54:978-981

Myers, R. A. and G. Mertz. 1998. Reducing uncertainty in the biological basis of fisheries management by meta-analysis of
data from many population: a synthesis. Fisheries Research 37:51-60.

Nonacs, P., P. E. Smith, A. Bouskila, and B. Luttberg. 1994. Modeling the behavior of the northern anchovy, Engraulis, as a
schooling predator exploiting patchy prey. Pp 147-170 in "U. S. GLOBEC: Global Ecosystems Dynamics" J. E. Eckman, ed.
Deep-Sea Research Part II 41:1:1-227

Nonacs, P., P. E. Smith, and M. S. Mangel. 1998. Modeling foraging in the northern anchovy (Engraulis mordax): individual
behavior can predict school dynamics and population biology. Canadian Journal of Fisheries and Aquatic Sciences
55:5:1179-1188

Ohman, M. D., G. H. Theilacker, and S. E. Kaupp. 1991. Immunochemical detection of predation on ciliate protists by larvae
of the northern anchovy (Engraulis mordax). Biological Bulletin 181:500-504

Owen, R. W. 1980. Eddies of the California Current System: Physical and Ecological Characteristics. Pp 237-263 [In] The
California island: proceedings of a multi disciplinary symposium. D. Power (ed) Santa Barbara Museum of Natural History pp
787

Owen, R. W. 1981. Fronts and eddies in the sea: mechanisms, interactions, and biological effects. Pp 197-233 In: Analysis of
Marine Ecosystems, A. R. Longhurst (ed) New York: Academic Press

Pares-Sierra, A., W. B. White, and C.-K. Tai. 1993. Wind-driven coastal generation of annual mesoscale eddy activity in the
California Current. Journal of Physical Oceanography 23:1110-1121

Paulik, G. J. 1973. Studies of the possible form of the stock-recruitment curve. Rapp. P.v. Reun. Cons. Int. Explor. Mer
164:302-315.

Pelaez, J. and J. A. McGowan. 1986. Phytoplankton pigment patterns in the California Current as determined by satellite.
Limnology and Oceanography 31:927-950.

Peterman, R. M., M. J. Bradford, N. C. H. Lo, and R. D. Methot. 1988. Contribution of early life stages to interannual
variability in recruitment of northern anchovy (Engraulis mordax). Can. J. Fish. Aquat. Ci. 45:8-16

Reid, J. L. 1962. On the circulation, phosphate-phosphorus content, and zooplankton volumes in the upper part of the Pacific
Ocean. Limnology and Oceanography 7:287-306

Reid, J. L. 1988. Physical Oceanography, 1947-1987. CalCOFI Rep. 29:42-65

Reid, J. L., G. I. Roden, and J. G. Wyllie. 1958. Studies of the California Current System. CalCOFI Rep. 6:27-56

Richards, L. J. and J. Maguire. 1998. Recent international agreements and the precautionary approach: new directions for
fisheries management science. Canadian Journal of Fisheries and Aquatic Sciences 55:6:1545-1544

Riffenburgh, R. H. 1969. A stochastic model of interpopulation dynamics in marine ecology. Journal of the Fisheries Research
Board of Canada 26:2843-2880

Rocha-Olivares, A. and R. D. Vetter. 1999. Effects of oceanographic circulation on gene flow, genetic structure, and
phylogeography of the rosethorn rockfish (Sebastes helvomaculatus). Canadian Journal of Fisheries and Aquatic Sciences
56:5:803-813

Roemmich, D. and J. A. McGowan. 1995a. Climatic warming and the decline of zooplankton in the California Current.
Science 267:1324-6

Roemmich, D. and J. A. McGowan. 1995b. Sampling zooplankton: correction. Science 268:352-353

Roessler, C. S. and D. B. Chelton. 1987. Zooplankton variability in the California Current, 1951-1982. CalCOFI Rep.
28:59-96

Sette, O. E. 1959. The long term historical record of meteorological, oceanographic and biological data. CalCOFI Rep.
7:181-194

Shenk, T. M., G. C. White, and K. P. Burnham. 1998. Sampling-variance effects on detecting density dependence from
temporal trends in natural populations. Ecological Monographs 68:445-463

Sissenwine, M. P. 1984. Why do fish populations vary? In Exploitation of marine communities, R. M. May, ed. Berlin:
Springer-Verlag, pp. 59-94.

Smith, P. E. 1978. Biological effects of ocean variability: time and space scales of biological response. Rapp. P.-v. Rèun.
Cons. Int. Explor. Mer, 173:117-127

Smith, P. E. 1995. Development of the population biology of the Pacific hake, Merluccius productus. CalCOFI Reports
36:144-152

Smith, P. E., M. D. Ohman, L. E. Eber. 1989. Analysis of the patterns of zooplankton aggregations from an acoustic doppler
current profiler. CalCOFI Reports 30:88-103

Smith, P. E., N. C. H. Lo., and J. L. Butler. 1992. Variation of life stage duration and survival

parameters as related to
interdecadal population variability in Pacific sardine. CalCOFI Reports 33:41-49

Smith, P. E. and H. G. Moser. 1988. CalCOFI Time series: an overview of fishes. CalCOFI Rep.
29:66-78

Soutar, A. and J. D. Isaacs. 1974. Abundance of pelagic fish during the 19th and 20th centuries
as recorded in anaerobic
sediment off the Californias. Fishery Bulletin, (U.S.) 72:257-274

Spencer, P. D. and J. S. Collie. 1997. Patterns of population variability in marine fish stocks.
Fisheries Oceanography
6:188-204

Strong, D. R. 1986. Density vague population change. Trends in Ecology and Evolution 1:39-42

Swartzman, G. L., W. M. Getz, R. C. Francis, R. T. Haar, and K. Rose. 1983. A management
analysis of the Pacific whiting
(Merluccius productus) fishery using an age-structured stochastic recruitment model. Canadian
Journal of Fisheries and
Aquatic Sciences 40:524-539

Swartzman, G. L., R. Brodeur, J. Napp, D. Walsh, R. Hewitt, D. Demer, G. Hunt, and E. A.
Logerwell. MS. Relating spatial
distributions of acoustically determined patches of fish and plankton: Image analysis, data
viewing and spatial proximity. Can. J.
Fish. Aquat Sci. XX:XXXX

Walsh, J. J., T. E. Whitledge, W. E. Esaias, R. L. Smith, S. A. Huntsman, H. Santander, and B. R.
De Mendiola. 1980. The
spawning habitat of the Peruvian anchovy, Engraulis ringens. Deep-Sea Research 27A:1-27

Watanabe, Y., H. Zenitani, and R. Kimura. 1996. Offshore expansion of spawning of the
Japanese sardine, Sardinops
melanostichus, and its implication for egg and larval survival. Canadian Journal of Fisheries and
Aquatic Sciences 53:55-61.

Ware, D. M. and R. E. Thomson. 1991. Link between long-term variability in upwelling and fish
production in the northeast
Pacific Ocean. Canadian Journal of Fisheries and Aquatic Sciences 48:2296-2306

Ware, D. M. and G. A. McFarlane. 1989. Fisheries production domains in the northeast Pacific
Ocean, p. 359-379. In R. J.
Beamish and G. A. McFarlane [eds.] Effects of ocean variability on recruitment and an evaluation
of parameters used in stock
assessment model. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Wilson, C., S. Pierce, P. M. Kosro, M. Dorn, and R. Smith. 1997. Ocean currents and the
distribution of Pacific whiting
(Merluccius productus) along the Pacific coast during summer, 1995. p 141-142 in 'Changing
Oceans and changing fisheries:
environmental data for fisheries research and management' G. W. Boehlert and J. D.
Schumacher [eds.]
NOAA-TM-NMFS-SWFSC-239