Pacific Ocean climate change: atmospheric forcing, ocean circulation and ecosystem response

Thomas L. Hayward

A major climate change event that affected atmospheric forcing, ocean circulation and ecosystem structure of the Pacific Ocean began in the mid-1970s. Changes in biomass, and presumably productivity, of the lower trophic levels (phytoplankton and zooplankton) were directly attributed to this event. It also appears that some individual species at higher trophic levels were influenced, but cause-and-effect relationships are more difficult to document at the species level. Recent work shows that at least five major pelagic ecosystems responded to this event, but in different ways, and both increases and decreases in biomass were seen. Changes of this magnitude are well documented in the paleo-oceanographic record. However, it remains to be determined to what extent the changes were caused by natural cycles versus anthropogenic change (global warming).

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At least five ecosystems, including the subtropical gyre of the North Pacific (the Central North Pacific), the Subarctic Pacific, the Kuroshio–Oyashio current system off Japan, the California Current and the Peru Current were affected by the mid-1970s climate change event (Fig. 1). Change on this scale is superimposed upon the higher-frequency fluctuations associated with El Niño, interannual and seasonal timescales. Change was observed in the basin-scale patterns of atmospheric forcing[1–4], circulation and physical structure of the ocean[5–7], and ecosystem structure[8]. Analysis of 40 long-time-series, including measurements of properties such as stream flow and the abundance of nesting geese, showed that terrestrial ecosystems were also affected by a step change at this time[9].

The paleo-oceanographic record indicates that changes of a similar magnitude and nature have regularly occurred over at least the past 2000 years[10]. However, the mid-1970s event is remarkable and it merits further consideration. It was ecologically significant because the changes were large when considered in the context of variability observed on other spatio-temporal scales. Because it is contemporary and may even still be evolving, the mid-1970s event has been observed differently and in more detail than previous events. It now appears more likely that global change is affecting the Earth's climate[11], therefore the question of whether the climate event of the mid-1970s is a natural cycle, or whether some component is due to global change, becomes even more important.

The spatial pattern of atmospheric forcing over the Pacific basin changed dramatically in the mid-1970s. The Aleutian low-pressure system shifted southward and intensified, resulting in an intensification of the westerly winds[2]. Sea surface temperature (SST) responded by increasing along the west coast of Alaska and North America, and decreasing in the Central North Pacific[4]. Mixed-layer depth (the isothermal layer at the surface of the ocean) became shallower in the Subarctic Pacific and deeper in the Central North Pacific[8]. The physical response of the ocean to changing atmospheric forcing is understood, at least to the extent that it can be reproduced in numeric simulations[3]. Changes in upper ocean temperature and mixed-layer depth affect primary production by altering the light and nutrient concentration to which the phytoplankton are exposed.

Other aspects of the physical structure of the ocean also changed in the mid-1970s. However, interpretation of these patterns is complicated. It is often unclear whether the change in a property represented by an index has a direct effect upon ecosystem structure, or whether it is simply correlated with change in some other more-direct forcing factor and, thus, is more useful as a general index of climate change. The pattern of Sverdrup transport (the large-scale, wind-driven ocean circulation) of the subarctic and subtropical gyres also changed in the mid-1970s[12]. In the waters off Japan, the southernmost latitude of the first Oyashio intrusion (an index of oceanographic structure that is correlated with environmental conditions in the coastal waters) was displaced southward for a period beginning in the mid-1970s and extending to at least the late 1980s[12]. Time-series of sea-level atmospheric pressure suggest that at least some aspects of atmospheric forcing were part of a decade-scale cycle, which had reversed by the late 1980s[4,8]. Contrary to these indications of a natural cycle, sea level and SST in the waters off California, USA have shown a secular increase that may be continuing and be related to global change[5–7].

Climate change and pelagic ecosystems

Pelagic biogeography and the boundaries of the major planktonic ecosystems of the Pacific Ocean are related to the circulation pattern and physical structure of the upper ocean[13]. The locations of the five major systems considered here are shown in Fig. 1.

California Current

The effects of climate change upon pelagic ecosystems may be better documented in the California Current region than elsewhere due to almost half a century of oceanographic and environmental data collected by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program[14]. Change in pelagic ecosystems occurs on a range of spatio-temporal scales and the relation between physical forcing and ecosystem response is scale dependent[15]. Low-frequency (interannual and longer) changes in plankton

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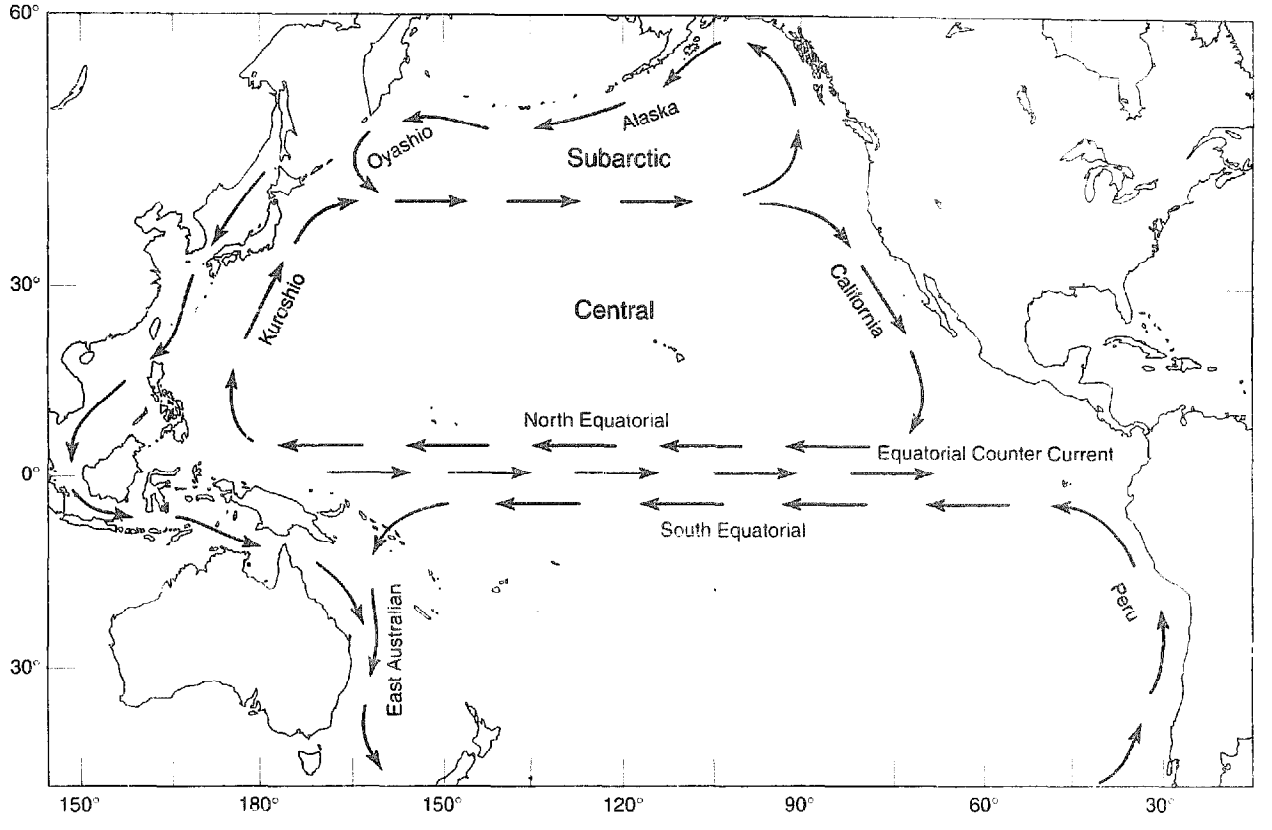

Fig. 1. Surface currents of the Pacific Ocean and location of the major pelagic ecosystems considered here (see shading).

abundance are important because they dominate the variance in long time-series. Changes on this scale are strongly correlated with indices of physical structure (such as upper ocean temperature and salinity) and the circulation pattern, suggesting that there is a cause-and-effect relationship between physical forcing and plankton abundance[16]. Starting in the mid-1970s, SST in the California Current increased[6]. Sea level (an index of ocean circulation, which is influenced by upper ocean temperature and salinity) increased in association with the warming of upper layers[5]. The upwelling index (an estimate of the strength of upwelling favorable winds responsible for bringing deeper, nutrient-rich waters to the surface) also increased in the mid-1970s, suggesting that there were stronger, upwelling favorable winds[1]. The observations of increased temperature, sea level and upwelling are contradictory; increased upwelling would be expected to cool the upper layers and lower sea level, the opposite of the observed trend[6]. These contradictory indications illustrate the difficulties in determining the specific processes that cause ecosystems to respond to climate change.

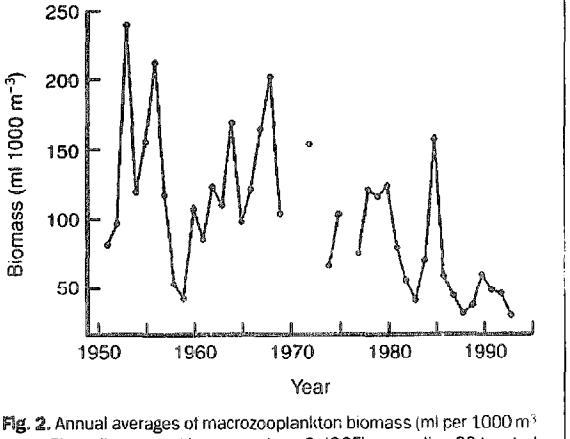

Fig. 2. Annual averages of macrozooplankton biomass (ml per 1000 m^3 water filtered) averaged in space along CalCOFI survey line 90 located off Southern California, USA. *Redrawn, with permission, from Ref. 7.*

Coincident with the changes in physical structure of the California Current, there was a sharp decrease in macrozooplankton biomass which started in the mid-1970s[6,7] (Fig. 2). By the early 1990s, macrozooplankton had decreased by 70% in comparison with levels of the 1960s. The decline in macrozooplankton continued into 1995 (Ref. 14). Long-term change in other aspects of ecosystem structure is not as well documented, but pelagic seabirds in the California Current have been declining for the past eight years[17]. This decrease is consistent with forcing by climate change, but there is no direct evidence of a link to the mid-1970s event. Additional evidence suggests that production of the kelp forests in the coastal waters of southern California, USA decreased in association with the mid-1970s event[18].

A nearly 2000-year record of the abundance of sardine (*Sardinops sagax*) and anchovy (*Engraulis mordax*) in the California Current was made by sampling the fish scales preserved in the anoxic sediments of the Santa Barbara basin where annual layers can be resolved[10]. Decadal-scale changes in the abundance of these species are strongly correlated with climate change. Changes of the magnitude of the 1975 event are well represented in the record long before anthropogenic climate change became an issue (Fig. 3).

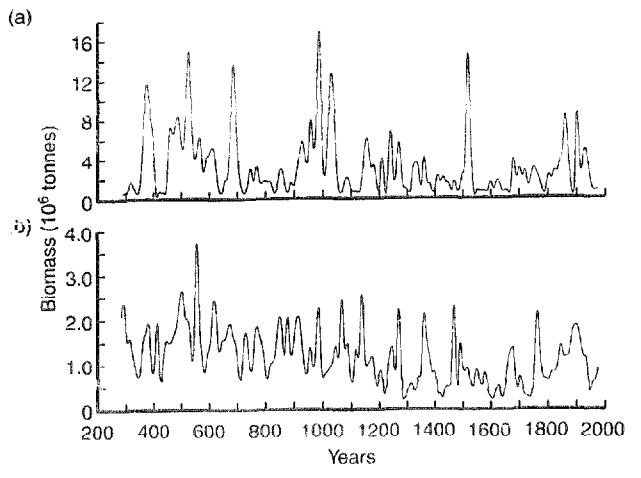

Fig. 3. 1700-year hindcast of estimated biomass (in millions of tonnes) of (a) Pacific sardine (*Sardinops sagax*) and (b) northern anchovy (*Engraulis mordax*) off California, USA and Baja California, Mexico, respectively. *Redrawn, with permission, from Ref. 10.*

The Kuroshio–Oyashio current system

Interannual variations in SST, sea surface salinity and the location of the boundary between the Kuroshio and Oyashio currents are strongly affected by atmospheric forcing and climate change. From the mid-1970s to recent years, the Oyashio has penetrated further south than previously in association with changes in the location of the Aleutian Low[12]. Biomass of zooplankton in the Oyashio region dropped sharply at the same time[19].

Peru Current system

The surface waters of the Peru Current have been warming since the mid-1970s, and this persisted at least into the late 1980s[20]. The upwelling index has also increased since the mid-1970s[1], although, as off California, this is in apparent contradiction to the warming of the upper layers. Starting in the mid-1970s, there was a large decline in zooplankton biomass and the anchoveta (*Engraulis ringens*, the dominant pelagic fish)[21] (Fig. 4). These declines in biomass persisted at least into the late 1980s. However, not all groups responded in the same way. Sardine (*Sardinops sagax*) increased at the same time as anchoveta declined, mackerel (*Scomber japonicus* and *Trachurus murphyi*) abundance did not show any trend from the mid-1950s to the mid-1980s, and pinnipeds showed a secular increase from the mid-1950s to the mid-1980s[21].

Central North Pacific

The Central North Pacific responded to climate change differently than the coastal ecosystems. Sea surface temperature cooled and winter winds increased in the mid-1970s[22]. Mixed-layer depth increased at the same time[8,23]. Based upon a time series of sea-level atmospheric pressure[23], it was suggested that this event 'began in the mid-1970s, peaked in the early 1980s and returned to a pre-1975 level by 1988'. Data collected from 1968 to 1985 showed that a 50% increase in chlorophyll concentration appeared to start in the mid-1970s[22]. The productivity of several trophic levels including the abundance of coral reef fish and spiny lobsters (*Panulirus marginatus*), reproductive success in sea birds and the survival of monk seal (*Monachus schauinslandi*) pups declined from the mid-1980s to the present. This has been interpreted as an ecosystem response to a decline in productivity following a peak associated with the mid-1970s climate event[8,23]. Time-series data being collected by the Hawaii Ocean Time Series Program[24] (HOT) may provide a basis for determining whether these trends are continuing.

Subarctic Pacific

The Subarctic Pacific ecosystem also responded to this event. Mixed-layer depths were 20 to 30% shallower in the 1977–1988 period compared with depths in 1960–1976, perhaps as a result of the intensification of the Aleutian Low (see Ref. 8). Zooplankton biomass in 1980–1989 was double that in 1956–1962 (Ref. 25). Long-term changes in the production of the three dominant species of salmon in this system are also correlated with each other and with temporal changes in the Aleutian Low system[26]. Total salmon catch increased dramatically in the mid-1970s. Changes in the upper trophic levels are attributed to bottom-up forcing via changes in mixed-layer depth, which are argued to affect directly primary production[8] and zooplankton production[26].

Ecological consequences of climate change

Understanding of the mid-1970s climate event is based upon data sets that were generally collected to examine other processes that occur on different spatio-temporal scales. The data have not been fully analyzed in the context of climate change and several important aspects of change remain poorly resolved. However, this event is contemporary, and more and different types of data were collected than were for previous events (which are largely known from the paleo-oceanographic record). Additional study would be useful because (1) events of this scale raise important issues for policy and management, and (2) it is not yet resolved to what extent such an event represents a natural cycle or global change.

The ability to attribute fluctuations in ecosystem structure to climate change, and to separate climate-driven processes from those occurring on different scales, such as fishing or environmental degradation, is important to understanding and managing ecosystems. Attribution of cause-and-effect relationships will require an improved understanding of how physical change affects ecosystems. Understanding the specific mechanisms linking climate change and ecosystems is also important for prediction of future ecosystem structure since progress in physical modeling has been more rapid than progress in ecosystem modeling.

One area of concern is determining which specific aspects of physical structure, such as wind stress[1], SST and stratification[6] or mixed-layer depth[8], have the most direct influence upon ecosystem structure. The nature of the linkages between physical and biological structure differs between ecosystems. Findings from one system cannot necessarily be extrapolated to others. Another area of concern is determining whether the effects upon ecosystem structure are direct, or if they involve bottom-up or top-down forcing. Change in ecosystem structure is generally presumed to be due to bottom-up forcing, in which physical structure affects primary production of the phytoplankton via changes in the nutrient distribution and stratification[1,6,8]. However, the situation is more complicated than is implied by a simple trophodynamic model. Observations in both Peru[21] and California[10] show that, within an ecosystem, similar species at the same trophic level may respond quite differently to climate change (e.g. Fig. 4). This indicates that other aspects of ecosystem structure may have a strong influence upon the abundance of individual species. Improving our understanding of the

linkages between climate change and population dynamics is an objective of the Global Ocean Ecosystems Dynamics (GLOBEC) program[27].

Another important and unresolved issue is whether the changes in ecosystem structure are part of a natural cycle, which will presumably reverse itself, or whether some component of the observed change is also associated with global change, which will not be reversible on the same timescales. The answer may again differ between ecosystems and for the specific aspect of ecosystem structure which is considered. Atmospheric forcing associated with changes in the Aleutian Low appears to have been part of a natural cycle that is reversing. Changes in productivity and salmon populations in the Central and Subarctic Pacific ecosystems also appear to have been at least partially cyclical in nature, and this cycle also appears to be reversing in at least the Central North Pacific. However, off California, the warming of the upper layers and the trend of low macrozooplankton biomass appears to be continuing into the mid-1990s.

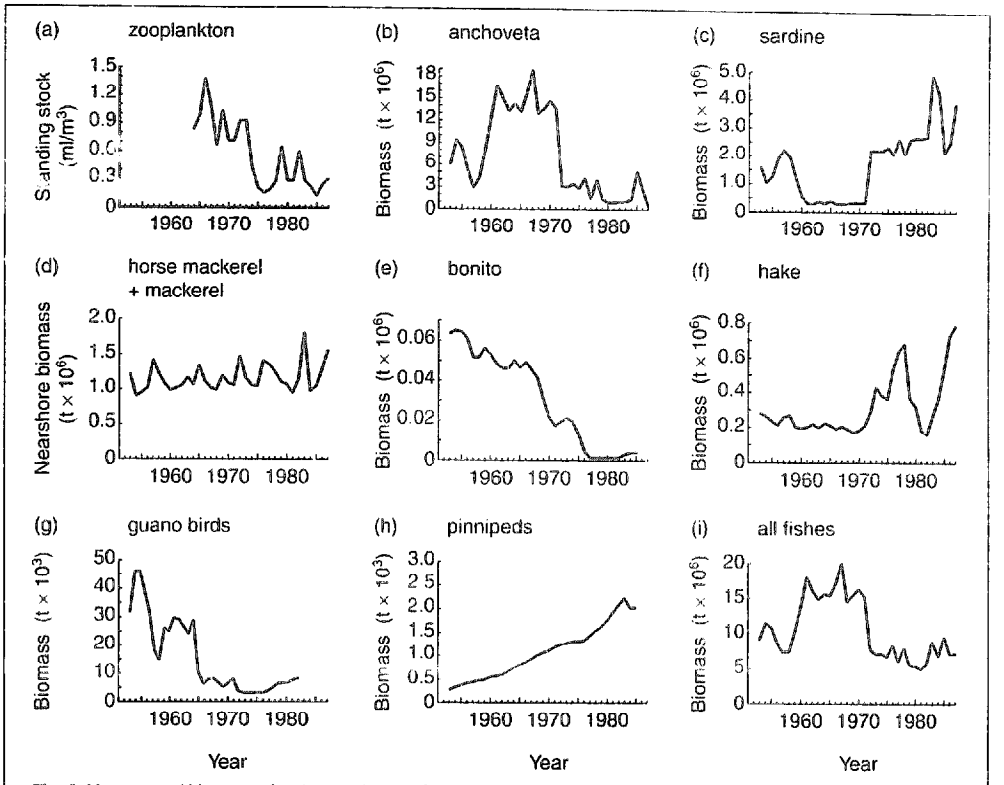

Fig. 4. Mean annual biomass of major species and functional groups in the region of the main distribution of the anchoveta from 4° to 14° S. *Redrawn, with permission, from Ref. 21.* (a) Zooplankton; (b) anchoveta, *Engraulis ringens*; (c) sardine, *Sardinops sagax*; (d) horse mackerel, *Trachurus murphyi*, and mackerel, *Scomber japonicus*; (e) bonito, *Sarda chileinsis*; (f) hake, *Merluccius gayi*; (g) guano birds; (h) pinnipeds; (i) all fishes.

The effects of climate change on species structure (as opposed to biomass) in pelagic ecosystems is also an important issue. At lower trophic levels, it is important to determine whether species structure (e.g. the order of abundance or spatial distribution) was affected by the climate event of the mid-1970s, and, if so, whether this affected other aspects of the ecosystem. This is important because it represents an additional mechanism by which climate change may influence higher trophic levels. Although this issue has not been adequately addressed for the plankton, the necessary samples exist for at least the California Current in the extensive collections made by the CalCOFI program. Changes in the abundance and productivity of individual species of higher trophic levels have been attributed to the mid-1970s climate event[8,26]. This event is also an example of a 'regime shift' in which ecosystems rapidly change from one 'state' to another. Regime shifts can be seen in the cyclical replacements of the dominant species in the fisheries of the California Current, Kuroshio and Subarctic ecosystems[28,29]. Time-series analysis shows that regime shifts tend to be correlated with indices of climate change, but directly attributing a cause-and-effect relation between environmental forcing and changes in the abundance of individual species is difficult owing to the confounding effects of harvesting and changes in range of large, mobile species. This difficulty is quite apparent in the very different time series of higher trophic levels in the Peru Current (Fig. 4).

Climate change events such as the one described here have implications for the ways in which pelagic ecosystems should be studied, as well as for policy and management. Even if events on this scale are not of direct interest in a particular management context, processes on other spatio-temporal scales (such as El Niño events, regional environmental degradation or point-source impacts) cannot be fully understood without accounting for variability on this spatio-temporal scale.

References

1 Bakun, A. (1990) **Global climate change and intensification of coastal ocean upwelling,** *Science* 247, 198–201

2 Graham, N.E. (1994) **Decadal-scale climate variability in the tropical and North Pacific during the 1970s and 1980s: observations and model results,** *Clim. Dyn.* 10, 135–162

3 Miller, A.J. *et al.* (1994) **Interdecadal variability of the Pacific Ocean: Model response to observed heat flux and wind stress anomalies,** *Clim. Dyn.* 9, 287–302

4 Trenberth, K.E. and Hurrell, J.W. (1994) **Decadal atmosphere–ocean variations in the Pacific,** *Clim. Dyn.* 9, 303–319

5 Roemmich, D. (1992) **Ocean warming and sea level rise along the south-west United States coast,** *Science* 257, 373–375

6 Roemmich, D. and McGowan, J. (1995) **Climatic warming and the decline of zooplankton in the California Current,** *Science* 267, 1324–1326

7 Roemmich, D. and McGowan, J. (1995) **Sampling zooplankton: correction,** *Science* 268, 352–353

8 Polovina, J.J., Mitchum, G.T. and Evans, G.T. (1995) **Decadal and basin-scale variation in mixed layer depth and the impact on biological production in the central and north Pacific 1960–88,** *Deep Sea Res.* 42, 1701–1716

9 Ebbesmeyer, C.C. *et al.* (1991) **1976 step in the Pacific climate: Forty environmental changes between 1968–1975 and 1977–1984,** in *Proceedings of the Seventh Annual Pacific Climate (PACLIM) Workshop, April 1990* (Betancourt, J.L. and Tharp, V.L., eds), pp. 115–126, (Interagency Ecological Studies Technical Report 26) California Department of Water Resources

10 Baumgartner, T.R., Soutar, A. and Ferreira-Bartrina, V. (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,** *CalCOFI Reports* 33, 24–41
11 Intergovernmental Panel on Climate Change (IPCC) (1996) *Climate Change 1995: The Science of Climate Change* (Houghton, J.T. *et al.*, eds), Cambridge University Press
12 Hanawa, K. (1995) **Southward penetration of the Oyashio water system and the wintertime condition of midlatitude westerlies over the North Pacific,** *Bull. Hokkaido Natl Fish. Res. Inst.* 59, 103–119
13 McGowan, J.A. (1974) **The nature of oceanic ecosystems,** in *The Biology of the Oceanic Pacific* (Miller, C.B., ed.), pp. 9–28, Oregon State University Press
14 Hayward, T.L. *et al.* (1996) **The state of the California Current in 1995: Continuing declines in macrozooplankton biomass during a period of nearly normal circulation,** *CalCOFI Reports* 37, 22–37
15 Haury, L.R., McGowan, J.A. and Wiebe, P.H. (1978) **Patterns and processes in the time-space scales of plankton distribution,** in *Spatial Patterns in Plankton Communities* (Steele J.H., ed.), pp. 277–327, Plenum Press
16 Chelton, D.B., Bernal, P.A. and McGowan, J.A. (1982) **Large-scale interannual physical and biological interaction in the California Current,** *J. Mar. Res.* 40, 1095–1125
17 Veit, R.R., Pyle, P. and McGowan, J.A. (1996) **Ocean warming and long-term change in pelagic bird abundance within the California Current System,** *Mar. Ecol. Prog. Ser.* 139, 11–18
18 Tegner, M.J. *et al.* (1996) **Is there evidence for long-term change in Southern California kelp forests?** *CalCOFI Reports* 37, 111–126
19 Odate, K. (1994) **Zooplankton biomass and its long-term variation in the western North Pacific Ocean, Tohoku Sea area, Japan,** *Bull. Tohoku Natl Fish. Res. Inst.* 56, 115–173
20 Brainard, R.E. and McClain, D.R. (1987) **Seasonal and interannual subsurface temperature variability off Peru, 1952 to 1984,** in *The Peruvian Anchoveta and its Upwelling Ecosystem: Three Decades of Change* (Pauly, D. *et al.*, eds), pp. 14–45, ICLARM Studies and Reviews 15, International Center for Living Aquatic Resources Management
21 Muck, P. (1989) **Major trends in the pelagic ecosystem off Peru and their implications for management,** in *The Peruvian Upwelling System: Dynamics and Interactions* (Pauly, D. *et al.*, eds), pp. 386–403, ICLARM Conference Proceedings 18, International Center for Living Aquatic Resources Management
22 Venrick, E.L. *et al.* (1987) **Climate and chlorophyll-a: Long-term trends in the central North Pacific ocean,** *Science* 238, 70–72
23 Polovina, J.J. *et al.* (1994) **Physical and biological consequences of a climate event in the central North Pacific,** *Fish. Oceanogr.* 3, 15–21
24 Karl, D.M. and Lukas, R. (1996) **The Hawaii ocean time-series (HOT) program – background, rationale and field implementation,** *Deep Sea Res.* 43, 129–156
25 Brodeur, R.D. and Ware, D.M. (1992) **Long-term variability in zooplankton in the subarctic Pacific Ocean,** *Fish. Oceanogr.* 1, 32–38
26 Beamish, R.J. and Bouillon, D.R. (1993) **Pacific salmon trends in relation to climate,** *Can. J. Fish. Aquat. Sci.* 50, 1002–1016
27 U.S. GLOBEC (1996) *Report on climate change and carrying capacity of the North Pacific ecosystem,* U.S. Global Ocean Ecosystem Dynamics Report 15
28 Francis, R.C. and Hare, S.R. (1994) **Decadal-scale regime shifts in the large marine ecosystems of the North-east Pacific: a case for historical science,** *Fish. Oceanogr.* 3, 279–291
29 MacCall, A.D. (1996) **Patterns of low-frequency variability in fish populations of the California Current,** *CalCOFI Reports* 37, 100–110

Sexual conflict resulting from adaptations to sperm competition

P. Stockley

Recent research on diverse animal taxa has revealed that male adaptations to sperm competition often lead to a conflict with female interests. That is, male attempts to increase their own fertilization success can result in a reduction of female fitness. This sexual conflict has led to selection for a variety of female adaptations that apparently reduce male-imposed costs. Understanding the causes and consequences of sexual conflict arising from adaptations to sperm competition offers much potential for new insight into the coevolution of male and female sexual strategies.

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Research into the evolutionary consequences of sperm competition has expanded rapidly in the 25 years since the field's inception[1]. Recently, work in this area has begun to reflect a broader trend towards consideration of female reproductive strategies. In particular, a growing number of studies now demonstrate how male strategies aimed at preventing or succeeding in sperm competition can lead to a conflict of interests between the sexes (Box 1). Often, adaptations for increasing male fertilization success result in a reduction of female fitness, thereby creating selection pressure on females to avoid or reduce male-imposed costs[2,3]. These sexual conflicts offer important insight into selection pressures shaping the evolution and function of female sexual strategies and, ultimately, coevolution of sexual strategies between the sexes. Here I assemble diverse examples of sexual conflict resulting from male adaptation to sperm competition, emphasizing the likely costs incurred by females and their response, if any, to the conflict.

Physical impairment or harm caused to females

Mate-guarding

Certain male adaptations for preventing sperm competition involve direct physical contact with, and/or close and persistent guarding of, females. Intense guarding often functions to prevent or delay additional copulations, thereby reducing the risk of sperm competition and increasing a male's chances of fertilization success[1]. However, while females may gain benefits from male guarding such as a reduction in harassment, close or persistent mate-guarding can be costly, owing to restrictions imposed on females' foraging and/or predator avoidance behaviour[4,5]. Moreover, where direct contact is involved, as in cases of prolonged copulation

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